the human population subsists on imported polished rice (Hirst, 1933, pp. 93–4), *X. cheopis* is mostly found on this rat. The fact that in Colombo (Hirst, 1927*a*, p. 346), where the domestic rats in the residential areas are exclusively parasitized by *X. astia*, *X. cheopis* is found on rats in the mercantile premises where piece goods, hardware and dry goods are stored, suggests that wherever a poor larval diet is available in the nest of the domestic rat only *X. cheopis* can thrive.

The fact that the larvae of the three Indian species of rat-fleas can develop on proteins other than those of blood (see p. 255) along with vitamins of the B group is of great significance, as it ensures their fairly wide dispersal. The fact that larvae of *X. cheopis* and *X. brasiliensis* develop on wheat flour alone better than those of *X. astia* (Tables 1, 2) affords the first two species better opportunities of establishing themselves when transported with grain far from their original home. It is possibly for this reason that these species have an almost world-wide distribution (Buxton, 1941, pp. 119, 121), and are found in places wherever the environmental conditions are favourable for their breeding. *X. cheopis*, whose original home appears to be the Mediterranean subregion, has extended to moderately cold regions almost all over the world, and has been recorded from places between 40° N. and 40° S. (Sharif, 1930, p. 47). *X. brasiliensis*, which is the second most widely distributed species of the genus (Hirst, 1927*a*, p. 283), having its ancestral home in the plateaux of the Ethiopian region and perhaps of the Ceylonese subregion, has spread to the tablelands of Peninsular India and the seaboard of the continent of America. On the other hand, a comparatively poor growth of the larvae of *X. astia* on wheat flour even in the presence of a slight fungous growth which is only possible at relative humidities higher than 70% (Fraenkel & Blewett, 1943*b*, p. 467), militates against a very wide dispersal of this species through the grain trade in the absence of its hosts. Consequently, *X. astia* has a restricted distribution, confined to the lowlands of the southern Asiatic countries (Hirst, 1926, p. 162), and has not been able to establish itself on rodents of countries far from its original home, even though their climatic conditions may be favourable. Its ancestral home is the Indo-Chinese subregion, and perhaps the Indian and Ceylonese subregions, as it is preponderantly found on their wild rodents.

## VII. SUMMARY

The comparative nutritive value of dried horse blood, highly milled wheat flour devoid of bran, a mixed diet of blood and wheat flour and that of blood and yeast for the larvae of *Xenopsylla cheopis*, *X. brasiliensis* and *X. astia* was ascertained experimentally. Pure blood proved inadequate, probably because it is deficient in accessory food factors. The growth of their larvae on wheat flour alone was erratic; only partial success was obtained, and the adults emerged after long and irregular intervals. This I attribute to the association of micro-organisms, possibly fungi, with this food. A mixture of blood and wheat flour quickened their larval development, but it was not a satisfactory larval diet. Blood and yeast form an ideal food for all flea larvae.

It is concluded that larval diets, containing blood or wheat proteins and vitamins of the B group, are essential for the successful rearing of these rat-fleas, and that the proper sclerotization of the adult is due to the presence of haemoglobin in the larval food. The available data on the effects of diverse diets on the growth of flea larvae lend strong support to the conclusion that successful development depends on the presence of these vitamins in the food; it also leads me to think that their source in nature may be the association of micro-organisms with the food.

The larval food appears to be an important factor that governs the distribution and host preferences of different species of flea. The larvae of *X. astia* require the most nutritive diet. If a rich larval food is present in a rodent burrow, *X. astia* flourishes, as in the burrows of *Tatera indica* and *Bandicota malabarica*, and even in those of the domestic rats in certain regions. In contrast, the nutritional requirements of the larvae of *Xenopsylla cheopis* and *X. brasiliensis* are simple; thus they prosper readily in a burrow of the domestic rat, even where the nutritive value of the larval food is very low. As the temperature tolerance of *X. brasiliensis* is the lowest, this species is confined to some of the cooler regions.

The irregular distribution of the three species of rat-fleas inside India may be related to differences in the nutritional value of the varied organic substances found in rat burrows in different places. The fact that the distribution of *X. cheopis* and *X. brasiliensis* is wider than that of *X. astia* is attributed to the ability of the larvae of the first two species to grow better on flour alone; this possibly enables them to survive transport in grain, even without rats, to places far from their original home.

I am much indebted to my chief, Lt.-Col. Sir Sahib Singh Sokhey, Director, Haffkine Institute, Bombay, for affording me many facilities for the pursuit of these investigations, and for his encouragement and advice. Prof. P. A. Buxton, F.R.S., has kindly read through and revised my manuscript and made many valuable suggestions, for which I am obliged to him. I am also obliged to Sir John Taylor for going through the manuscript.

I take this opportunity of acknowledging my

Sorghum (*Andropogon sorghum*), spiked millet (*Pennisetum typhoideum*) and cotton are the main agricultural products of these regions. Cattle fodder is mostly the dried stalks of the two millets, which are stored in stacks in the backyards of houses, and are often utilized by domestic rats to build their nests. The nesting conditions of domestic rats in these regions provide such a poor diet for flea larvae that only *Xenopsylla cheopis* can prosper.

The primary factor affecting the distribution of *X. brasiliensis* is temperature, as the upper temperature limit of its larval development is lower than those of two other species (Sharif, 1948). As mentioned before (see p. 255), its larvae developed best on a diet composed exclusively of wheat flour, which suggests that the vitamin B requirements of the larvae of this species are the lowest. Consequently, this flea mostly abounds in grain stores of cooler places, such as Mysore City, Davanagee, Sagar, Shimoga in the Mysore State (Iyer, 1933, pp. 984–93). This species appears to be common only in the predominantly millet- and rice-growing cooler elevated tablelands of Peninsular India. On the watersheds of the Western Ghats in the Dharwar taluk, it was often found in big commercial towns, but not in the adjoining villages. Its tolerance of a low temperature probably accounts for this disparity in the distribution. Granaries in big towns are well protected against the sun, which is not the case in small villages.

*X. brasiliensis* is entirely absent in the lowlands of Peninsular India. Its distribution is mainly restricted to the tablelands of Peninsular India and Africa (Buxton, 1941, p. 121), and belts of plains with high temperature have limited its dispersal. Thus its distribution is controlled to a large extent by climatic barriers and zoogeographical principles.

The larvae of *X. astia* are tolerant of a higher temperature than those of the other two species (Sharif, 1948). Patton & Evans (1929, p. 534) suggested that the 'optimum conditions for its life processes are a somewhat higher temperature than *cheopis* and a high atmospheric humidity'. The nutritional requirements of the larvae of *X. astia* being higher than those of the other two species, they require food rich in vitamins of the B group, and possibly in proteins also. Consequently, a higher water content in the food may be needed so as to encourage growth of fungus, which appears to be essential for their development.

*X. astia* is the flea of domestic rats in rice-growing warm and moist lowlands and plains of India bordering the Bay of Bengal and those of Burma and Ceylon (Hirst, 1927*a*, p. 326). Paddy (unhusked rice) or its husks and straws stored in houses are utilized by domestic rats for making nests. The husk of the paddy is fairly rich in vitamins of the B group, as the pericarp and a greater part of the embryo remain attached to it after the polishing of rice, and in humid and warm places fungus and other micro-organisms can easily flourish on such a litter. Consequently, being a stronger competitor in the struggle for existence than the other two species and able to withstand higher temperature, *X. astia* prospers in it.

Some of the villages of the Dharwar taluk that produced a small quantity of wheat, in addition to other cereals, had comparatively larger proportions of *X. astia* on their domestic rats than those that did not. Possibly, there is some association between wheat cultivation and this flea. McCarrison (1927, p. 636) showed experimentally that of the four important Indian cereals, viz. wheat, spiked millet, sorghum, paddy, the first has more nutritive value, both as regards proteins and vitamin B complex, than the others. These cereals can influence the different distribution of rat-fleas by providing larval food of different nutritive value in the burrows of their hosts (see p. 260). In the wheat-growing plains of the Punjab and the United Provinces *X. astia* is also found along with *X. cheopis* on domestic rats in fairly large proportions (Hirst, 1927*a*, pp. 380, 416), and at some places even the former species predominates (Cragg, 1921, 1923). In them wheat chaff and straw are utilized by domestic rats for making their nests, as they are usually stored in houses, and form the main fodder for cattle. Wheat straw and chaff, when kept even in a moderately wet soil, encourage growth of micro-organisms.

In view of this analysis of the burrow conditions of different rodents, it is reasonable to suggest that the irregular distribution of the three species of rat-fleas, especially that of *X. cheopis* and *X. astia*, in India (see Hirst, 1927*a*, p. 381) is governed by the nesting conditions and nature of food of their hosts in combination with the climatic conditions. Wherever debris and litter, containing larval food rich in vitamins of the B group and perhaps in proteins, are present in the burrow of a rodent, either as the result of association of micro-organisms or owing to the presence of substances intrinsically rich in them, *X. astia* is the sole flea. This presumption is supported by the fact that domestic rats in the paddy-growing districts in the warm and moist regions around the Bay of Bengal, and *Tatera indica* and *Bandicota malabarica* in the Deccan Plateau are parasitized by *Xenopsylla astia*. In contrast, if the debris and litter contain larval food with low concentration of these nutriments, as is found in the burrows of the domestic rats of comparatively warmer regions of the Deccan Plateau, *X. cheopis* is exclusively found on them. It is possibly for these reasons that places in the plains of Bundelkhand (Hirst, 1927*a*, pp. 384, 399), the Madras Presidency (Hirst, 1925, p. 10), eastern Bengal, Assam and Burma (Hirst, 1927*a*, p. 392), where the human population lives on locally produced paddy, have *X. astia* as the preponderating species on the domestic rat; but in those places where

The distribution of the three Indian species of *Xenopsylla* and their host preferences can logically be explained on the basis of differences in the nutritional requirements of their larvae. It seems that the larvae of each of these species have certain minimum nutritional requirements. If the food available in a locality is lacking in any one of the required nutritive constituents for the larvae of a species, that insect will be absent. Fleas being mostly inhabitants of the nests and retreats of their hosts, their larvae are dependent upon the nutriment found in them. Organic substances found in the retreats of different rodents are variable (Sharif, 1948). Even in the domestic rat burrow, in addition to flea faeces, the organic matter found, which consists mostly of the nesting material and rat droppings, is very variable in diverse localities, being dependent on the agricultural products available. Furthermore, its nutritive value both in quality and quantity is greatly influenced by the prevailing weather conditions in an area (see Shelford, 1930, p. 101). If the burrow humidity is high, growth of micro-organisms, especially mould, will set in, which will enhance the nutritional value of the larval food. Important articles of diet for rat-flea larvae in nature are rat and flea faeces, but even the nutritive value of the faeces of domestic rats varies in different places. Undigested food particles are passed along with rat faeces; at different places various kinds of crushed grains and their husks, depending on the staple food of the inhabitants of the locality, have been seen in the faeces and stomach contents of rats.

The burrows of *Tatera indica* are very long and tortuous; they are also very deep, their depth varying from 24 to 54 in. The water content of the soil in such burrows must surely be high enough to encourage fungous growth on debris; indeed, I have personally seen moulds growing on the faecal pellets and nesting material of this rodent. It is suggested that the presence of fungus on the debris and litter of such burrows plays an important part in the enormous increase of the population of *Xenopsylla astia* in them. *Tatera indica* usually lives in colonies composed of 6–30 individuals in a complicated burrow system. There can be nothing better for enormous multiplication of *Xenopsylla astia*, as every necessary food constituent for flea larvae is present. Consequently, this flea is abundant in the burrows of *Tatera indica* to the entire exclusion of others throughout the year, and on a number of occasions one to two thousand fleas were recovered from its burrows.

Similarly, many individuals of *Bandicota malabarica* live in a complicated and tortuous burrow system, which is also very deep. The debris in it, especially in the resting chambers, is fairly wet. As a rule, this rodent does not build a nest; only a few sparsely scattered grains, shells of groundnuts, leaves, etc., in a fairly sodden state, with fungous growth on them, were found in the chambers. The flea population, consisting mostly of *Xenopsylla astia*, in each chamber was many times more than was found in a nest of the domestic rat.

Different subspecies of the domestic rat, *Rattus rattus* (Linnaeus), are good and permanent hosts of *Xenopsylla cheopis* in many parts of the world (see, for instance, Advisory Committee, 1908, p. 245; Hirst, 1927*a*, p. 335), especially in the tropical and subtropical countries. Wherever this flea is absent, it is because it is replaced by other hardier species. The depth of the burrows of this rat, examined in the taluks of Barsi and Dharwar, was variable. A typical underground burrow was not very deep, its depth hardly exceeding 20 in. The humidity of such a burrow kept under observation in the town of Dharwar for about a year, fluctuated mostly between 50 and 80 %; but it is liable to be lower in dry and higher in damp situations. The chances of fungous growth on the debris and litter of domestic rat burrows in both these taluks appear to be slight. Thus the available food for flea larvae in such burrows is unlikely to be rich in nutriment. Consequently, it might be adequate for the larvae of *X. cheopis*, but not for those of *X. astia*, whose nutritional requirements are higher (see p. 257). A few individuals of *X. astia* were found on the domestic rats of these taluks owing to their close association with *Tatera indica* or *Bandicota malabarica*; but they could not establish themselves on domestic rats on account of the poor larval food available in their burrows.

The association of *Xenopsylla cheopis* with grain in many parts of the world is well known (see Hirst, 1926, p. 163; 1927*a*, pp. 371, 398). The conditions prevailing in most granaries and warehouses are suitable for rearing of this species only (Hirst, 1927*b*, p. 94); in my opinion the debris present here has a low nutritive value and is inadequate for the larvae of *X. astia*. The presence of *X. cheopis* in the stores of polished rice, other grains and cotton in the mercantile premises of Rangoon (Jolly, Fenn & Dorai, 1931, p. 1236), certain trade centres in the plains of the Madras Presidency (King & Pandit, 1931, pp. 366, 369), and Colombo (Hirst, 1927*a*, pp. 344–7, 382; 1933, p. 93), where the indigenous flea on domestic rats found in the residential premises is exclusively *X. astia*, seems to be best explained by the low nutritional requirements of the larvae of *X. cheopis*; as a poor larval diet can only be available in granaries well protected against the humid climatic conditions of these areas. On the other hand, the rat burrows in residential premises in these areas provide a rich source of food on which the larvae of *X. astia* can flourish.

The plateaux of Peninsular India are regions where *X. cheopis* is abundant on domestic rats.

was observed in the breeding jars owing to dampness caused by high humidity during the rainy months. The presence of fungus always resulted in excessive increase of the flea population.

A burrow of the Indian domestic rat contains rat and flea faeces, also the nesting material composed of pieces of cloth, gunny bag and paper, strings of cotton, jute and coir, raw cotton, dry leaves and straws of fodder, etc. These items have not much nutritive value for flea larvae; and this probably accounts for a low flea infestation often found in such burrows, especially in dry situations. An appreciable increase in the flea population was observed during the rainy months, when fungous growth on debris and rat faeces in the burrow will occur. Possibly fungous growth, which only occurs at relative humidities higher than 70 %, serves an additional source of food. The fact that the larvae of the three Indian rat-fleas (Sharif, 1948) were reared on the mixed diet of blood and yeast at low humidities (50 and 60 %), suggests that in the presence of sufficient supply of vitamins of the B group, the association of micro-organisms with the diet to supply accessory food substances is not necessary. It is, therefore, suggested that under dry conditions the source of B vitamins may be different agricultural products that are either found in undigested form in the faeces of their hosts or intact in their burrows. If a larval food with a low concentration of these vitamins is available, as it would be in some rat burrows during dry and hot months, breeding of fleas on a small scale might continue.

## VI. INFLUENCE OF LARVAL FOOD ON THE SPECIFIC DISTRIBUTION AND HOST PREFERENCES OF THE THREE INDIAN RAT-FLEAS

The facts of distribution of *X. cheopis*, *X. brasiliensis* and *X. astia* in India are fairly fully known. They may be partly explained by zoogeography. There is no doubt of the fundamental importance of this factor; but it is difficult to see that it could continue to be important for the ectoparasites of the domestic rat which is dispersed so much through human agency. Trade through ships and other modes of transport plays a great part in the dispersal of these rat-fleas, either by transferring them from one place to another or through the agency of their hosts. Climatic conditions prevailing at a place of importation on the bionomics of fleas also control their distribution. I do not find that these factors suffice to explain the presence or absence of the three species of rat-fleas inside India. As fleas are temporary ectoparasites and inhabitants of the nests or retreats of their hosts, many species have become highly specialized not merely in regard to the blood of some particular host, but as to its nesting conditions. It may be that conditions in the burrow make great differences to larval nutrition and therefore to the absence, presence or abundance of flea species. Indubitably, the range of the possible diet of a flea larva is a wide one; but the larvae of all the species are not alike in their food requirements as 'some do not succeed on food that gives good results for others' (Bacot, 1914, p. 513). It is also known 'that no insect can develop on a food which is lacking even in one important constituent' (Fraenkel & Blewett, 1943*b*, p. 485). My own observations in the laboratory on the dietetic requirements of the larvae of different species of the Indian rat-fleas support these assumptions. In the field I have made observations on the rodent biology, which also seem to be relevant.

The examination of about 160,000 fleas of both wild and domestic rodents of the Barsi and Dharwar taluks for about 3 years, and the study of their burrow conditions, have enabled me to determine some factors that control the irregular distribution of the three Indian rat-fleas. These two well-separated taluks lying in the Deccan Plateau have different climatic conditions, Barsi being warmer than Dharwar. *X. cheopis* was predominantly found on the domestic rat, *Rattus rattus rufescens* (Gray), of the Barsi taluk. *Xenopsylla brasiliensis* was present only on the domestic rats, *Rattus rattus rufescens* and *R. rattus wroughtoni* (Hinton), of the cooler uplands of the Dharwar taluk along with *Xenopsylla cheopis*, where infestation of the former flea at some places amounted to 40–56 % of the total fleas. But *X. brasiliensis* was almost absent on these domestic rats of some of the adjoining warmer villages, even when situated within about 1–4 miles of those that had this species; in these villages *X. cheopis* was almost exclusively found as in the comparatively warmer regions of this taluk. On the other hand, *X. astia* was present to the exclusion of other fleas on the Indian gerbille, *Tatera indica* (Hardwicke), found in fields, and predominantly on *Bandicota malabarica* (Shaw) in houses, all over these two taluks. *Xenopsylla astia* was also present in very small proportions on the domestic rats of those houses that harboured *Bandicota malabarica*; but it was not found in houses free from this rodent. The fact that only *Xenopsylla cheopis* is found on domestic rats and *X. astia* on *Bandicota malabarica* in the same house, and that the latter flea is the only species found on the wild rodent, *Tatera indica*, in the same village, militates against the idea that the distribution of these fleas is governed exclusively by climatic factors (Taylor & Chitre, 1923, pp. 625–7), or by zoogeographical principles (Hirst, 1927*a*, pp. 317–30). It seems evident that in nature some other biological factor of a greater potency is operating: it is difficult, if not impossible, to escape the conclusion that this factor is the larval food.

necessary for the growing larvae to wait for importation and multiplication of micro-organisms to ensure their successful growth. It is, therefore, evident that this food fulfils the essential requirements of an ideal diet for the larvae of these species. Yeast by itself (Sharif, 1937, p. 233) has no food value for flea larvae. Possibly the yeast proteins are an inadequate diet for them; but yeast possesses growth-promoting substances, the vitamins of the B group. It appears that the native proteins of blood and B vitamins form an ideal food for flea larvae.

There is evidence from insects of many orders of the importance of vitamins of the B group; for the larvae of certain beetles and moths infesting stored products (Fraenkel & Blewett, 1943*a*, pp. 506, 507; Blewett & Fraenkel, 1944, p. 220), and the blow-fly larvae (Hobson, 1933, p. 1908; 1935, p. 1290) cannot grow without them. In these insect larvae the source of these vitamins is micro-organisms which synthesize them in the food. Similarly, it is suggested that when the available food of flea larvae is intrinsically deficient in B vitamins, the association of micro-organisms with it is essential for their normal development.

It seems possible that when fleas feed on a plague-infected rat their excrement, due to the presence of *Pasteurella pestis* (Advisory Committee, 1907*a*, p. 404), may contain materials unusually favourable to their larvae, if they happen to devour that excrement. In my view this may help to explain the great numbers of fleas which have often been observed on rats or trap guinea-pigs in plague-infected houses (see, for instance, Advisory Committee, 1907*b*, p. 443; Hirst, 1926, p. 221). It is, of course, admitted that other factors, e.g. favourable climate and concentration of fleas on a few surviving rats, contribute to the same result (see Hirst, 1926, p. 249; 1927*a*, p. 342); but the phenomenal increase of fleas that is usually found in plague-infected houses cannot be explained by these two factors alone. My assumption is strongly supported by the results of the 'pit experiments' of Webster & Chitre (1930, p. 706) on the transmission of plague by *Xenopsylla astia* and *X. cheopis*. The flea population in the pits increased to such an extent in about a month's time—a period enough for a single generation of fleas in the climate of Bombay—after the introduction of the plague-infected rats, that it caused a heavy mortality amongst rats owing to flea worry and excessive sucking of blood. Heavy infestation of sick rats with fleas, as has been observed by the Advisory Committee (1908, p. 254) and Bacot (1914, p. 472), might be due to the sick rats providing accessory food factors for the larvae of fleas, through the infection of blood with pathogenic micro-organisms.

Flea larvae usually feed on decaying organic matter containing micro-organisms, an association of micro-organisms with the larval food may therefore be essential to some species; but at present the evidence on this point is only indirect. The possibility that flea larvae ingest fungi* has been suggested elsewhere (Sharif, 1948). The exact nutritive value of fungi is as yet unknown; but according to Chapman (1931, p. 159), 'Plant and animal residue may be used more or less directly by the fungi; and the fungi, by the insect.' The fact that premises storing manure, composts and dungs are comparatively more heavily infested with fleas than those without them, indicates that saprophytic fungi may play some part in the increase of fleas.

The existence of 'lagging larvae' of the three Indian rat-fleas on a diet of wheat flour (see p. 255) is definitively suggestive of the occurrence of some gradual and favourable change in this food. Such larvae are the result of malnutrition (Sharif, 1937, p. 232) and not of diapause. The gradual growth of a small quantity of mould on the dead larvae and the food, which perhaps was only sufficient to bring a proportion of larvae to the adult stage, may have allowed others to live much longer than is normal. The marked disparity in growth rate of flea larvae might indicate slow and gradual supply of some other nutritive material to them, in addition to what was present in this food at the beginning of the experiment.

Earlier workers had great difficulty in getting consistent results in breeding flea larvae. In my opinion the partial and variable success in rearing flea larvae obtained by Bacot (1914), Webster (1930) and Sikes (1931) on different diets, but only at a relative humidity of about 70 % and higher, was due to the presence of a few micro-organisms, possibly fungi, in the food at some later stage. The fact that a higher percentage of mortality occurred in the beginning of my experiments (see p. 255) supports this assumption.

In nature in a domestic rat burrow I have never come across such an enormous flea population as was found in my breeding jars. Each jar had sea sand and wheat grain, to which a little dried horse blood and yeast was added. For feeding adult fleas a white mouse was put in a jar with a water supply, as described by Leeson (1932, p. 26). The flea population in each jar often increased to such an extent that surplus fleas had to be removed several times a year in order to avoid the death of the mouse. The jar contained only flea and mouse faeces, partially eaten wheat grain, and a small quantity of blood and yeast. In addition, slight putrefaction and fungus growth

* Major W. L. Jellison, of the United States Public Health Service, on a visit to the Haffkine Institute about three years ago, informed me that he has seen on several occasions spores and hyphae of fungi in the alimentary canal of flea larvae. According to him, they are more often found in the gut of the larvae of wild rodent fleas.

these two diets and no statistical difference existed in their length measurements confirms the previous conclusion (see p. 256) that addition of blood to flour has not resulted in improvement in rearing of its larvae.

The average length of a few adults of *X. cheopis* (Table 3), obtained from the larvae reared on blood alone, was not statistically different from that of those whose larvae were nourished on flour alone or the mixed diet of blood and flour. Only their average breadth was significantly less than that of adults from larvae on a mixture of blood and flour. These facts indicate that the larvae of this species that bred successfully on blood alone may have had an opportunity of obtaining a small amount of an accessory food substance.

It is, therefore, evident that the condition of the adults of the three Indian rat-fleas, as expressed by their length and breadth measurements, is also a good indication of the efficiency of the larval diets, and they confirm my conclusions based on the duration of larval life or combined larval and pupal life, and on the proportions of larvae which became pupae or adults.

## V. DIETETIC REQUIREMENTS OF FLEA LARVAE

It is now known that the food available to flea larvae consists of varied organic matter; but there is still no information regarding the actual food which they select. In order to throw light on their exact nutritional requirements, an attempt will now be made to collect and combine all the available information on the subject.

Blood is generally considered an integral part of the larval food for almost all the fleas. But my recent experiments on *X. cheopis*, *X. brasiliensis* and *X. astia* (Table 1), and earlier ones (Sharif, 1937, p. 231) on *Nosopsyllus fasciatus* (Bosc) show that sterile or pure, dried horse blood is an inadequate diet for the larvae of these species; on blood alone successful rearing of adults is not possible. Evidently blood lacks some important factor necessary for normal and successful breeding of them, which is compensated by the addition of yeast, or possibly when blood is contaminated with micro-organisms. The meagre success obtained in rearing flea larvae on blood alone (see p. 255) is attributed to the association of a few micro-organisms with blood due to a chance contamination, which increases its nutritive value by providing vitamins of the B group, as in *Rhodnius prolixus* Stål (Wigglesworth, 1936, p. 289; Brecher & Wigglesworth, 1944, p. 224). Sikes (1931, p. 247) obtained partial and highly variable success in rearing flea larvae on blood at 80 and 90 % R.H. The contradictory results obtained on this or other diets by different workers may be due to the fact that flea larvae have never been reared on sterile food.

My work also shows (Tables 1, 2) that highly milled wheat flour without bran is an unfavourable larval diet for the three Indian species of *Xenopsylla*. There is a high mortality and great irregularity in development; moreover, adults are small (Table 3) and pale yellow. It seems that the larvae swallow much of the flour, but they do not digest it completely, perhaps because their principal requirements are proteins and vitamins. To what extent slight fungous growth on dead larvae or on the flour itself is a source of vitamins or energy I do not know.

The addition of blood to wheat flour, however, shortened the larval life of the three Indian rat-fleas a good deal (Tables 1, 2), and a comparatively larger number of their larvae completed the active larval life, and without irregularity; this indicates that the mixed diet is in some way more suitable. The fact that a few larvae of *X. cheopis* that bred successfully on blood alone had significantly shorter active larval, and resting larval and pupal life than when its larvae were fed on wheat flour alone, suggests that flea larvae require food rich in nitrogenous substances. The mixed diet of blood and wheat flour, however, lacks some important factors; it is probable that these are vitamins of the B group, and they could not be supplied in adequate amount owing to the desiccating influence of 80 % R.H. on this diet, and also owing to the initial inadequacy of them in the highly milled wheat flour devoid of bran. The comparatively poor development of the larvae of *X. astia* on the mixed diet of blood and wheat flour and on wheat flour alone may indicate that the vitamin B requirements of its larva are exceptionally high.

The adults obtained from the larvae of the three species when nourished on the mixed diet of blood and wheat flour were deep brown and fully sclerotized, unlike those whose larvae fed on wheat flour alone. The absence of proper sclerotization in the adults of *Nosopsyllus fasciatus*, when its larvae were fed on serum and yeast (Sharif, 1937, p. 232), and the development of normal colour in those whose larval diet contained red corpuscles or haemoglobin along with yeast, clearly indicate that these materials contain something, possibly iron, which promotes proper sclerotization. In this connexion it is pointed out that the larvae of *N. fasciatus*, when fed on yeast and serum, to which ferrous ammonium sulphate [$FeSO_4(NH_4)_2SO_4 . 6H_2O$] was added in the same concentration as iron in the haemoglobin, yielded properly sclerotized adults.*

A mixed diet of blood and yeast gave the most rapid development of the larvae of the three species (Tables 1, 2), with almost 100 % emergence of adults, which were normally sclerotized. Possibly owing to the high nutritive value of this mixed diet, it was not

* This fact was not mentioned in my earlier communication (Sharif, 1937), as it escaped my attention then.

The general behaviour of flour exposed to the atmospheric humidity of 80 % denotes that it absorbed more water than the dried blood. The former adhered to the larvae, but not to such an extent as the latter. The flour definitely increased in volume; but it looked slightly moist and discrete after 141 days' exposure to this humidity. If not disturbed for a number of days, it formed a loosely held brittle mass with sand, and a thin crust was formed on the surface. When the larvae were present in the tube, the surface of the food and sand mixture was always covered with a large quantity of frass in the form of fluffy flour. The larvae fed on this food were sluggish, and only those that remained within cocoons bred successfully. The ability of some larvae to spin cocoons shows that flour at 80 % R.H. contains enough moisture to permit of cocoon formation. The cocoons formed by the larvae fed on flour were smaller and softer, having looser meshes, than those spun by larvae fed on the mixed diet of blood and yeast; this seems to show that the former food had less moisture content than the latter (Sharif, 1948).

(c) *Blood and wheat flour*. On this mixed diet (Tables 1, 2) 54·4 % larvae of *X. cheopis* and 48·4 % of *X. brasiliensis* pupated, and the remainder died in the resting stage after completion of their active larval life. In contrast, only 58·2 % of the larvae of *X. astia* completed their active larval life, and 40·7 % of them pupated. Only 21·3 % larvae of *X. cheopis*, 9·7 % of *X. brasiliensis* and 24·2 % of *X. astia* were reared into adults. The addition of blood to flour resulted in a considerable shortening of the combined larval and pupal life of the three species.

A statistically higher mortality rate in the larval stage and longer average active larval life on this mixed diet in *X. astia* (Tables 1, 2) than in the other two species, indicate that its larvae have more particular nutritional requirements; moreover, the food, at 80 % R.H., may give a less favourable atmospheric condition. But a significantly shorter resting larval and pupal life in *X. astia* than in the other two species, suggests that those of its larvae which became adults were able to obtain more nutritive food owing to their prolonged larval life; possibly the nutritional value of the food improved with the length of exposure to this humidity.

The proportions of adults of *X. cheopis* and *X. astia* (Table 1), when their larvae were reared on the mixed diet of blood and flour, were not significantly different from their proportions when reared on flour alone; similarly, no statistical difference existed in rearing of adults of both these species on the former diet. On the other hand, a significantly lower proportion of the larvae of *X. brasiliensis* reached the adult stage on this mixed diet than when they were fed on flour alone, and also than when the larvae of *X. cheopis* and *X. astia* fed on the former diet. This shows a more pronounced desiccating influence of the mixed diet on the pupae of *X. brasiliensis* than on those of both the other species, as the proportion of its pupation did not differ statistically from that of either of the other two species on this diet, and also from that when its larvae fed on flour alone. A marked desiccating influence of the mixed diet on the pupae of *X. cheopis* and *X. astia* is also demonstrated by the fact that in spite of the better growth of their larvae on it (in comparison with flour alone), there was no improvement in successful rearing of the adults.

There was a little cocoon formation on this mixed diet, and a fairly high mortality occurred in the pupal stage owing to loss of water. Adults of both the sexes emerged indifferently and after great difficulty from the pupal skins, and they were less active after emergence. These facts bear testimony to the dryness of this food.

Evidently, the nutritive value of this mixed diet is higher for the larvae of the three species than that of flour alone; but the desiccating influence of the former diet, kept at 80 % R.H., was responsible for a high rate of mortality.

The mixed diet of blood and flour increased slightly in bulk at 80 % R.H.; but it remained dry and discrete throughout an exposure of 86 days, and was dull red in colour. It adhered to the larvae and the pupae so largely that they looked almost covered with it. The larvae were very sluggish, and a large quantity of food was passed by them undigested.

(d) *Blood and yeast*. The combined larval and pupal life of the three species on the mixed diet of blood and yeast was much shorter than on flour alone or the mixed diet of blood and flour (Table 2), mainly due to a statistically great reduction in their active larval life. Evidently, the first diet has a much better nutritive value for flea larvae than the other two. The larval growth was regular on this mixed diet, as the interval between the first and the last cocoon formation was only 4–5 days. The percentage of cocoon formation was very high, and there was almost 100 % pupation and adult emergence (Table 1).

This mixed food seemed to gain more water than the others from the atmospheric humidity of 80 %; it did not adhere to the larvae and the pupae and was of bright red colour.

The dimensions (average lengths and breadths) of the adults of the three species (Table 3) reared from the larvae on blood and yeast were statistically much greater than those of the adults from the other diets.

The adults of *X. cheopis* and *X. astia* (Table 3), whose larvae fed on the mixed diet of blood and flour, were statistically longer and broader than those reared on flour alone; this indicates the better nutritive value of the former food. The fact that the breadth measurements of both the sexes of *X. brasiliensis* showed significantly inconsistent disparity on

were noted. A mixture of blood and yeast was used for control experiments, as it possesses all the essential requirements of an ideal food for flea larvae.

Sikes (1931, p. 245) has found that different kinds of food have different hygroscopic properties, and the optimum atmospheric humidity for rearing flea larvae varied according to the kind of food employed so as to satisfy their water requirements. The degree of moisture content of the different diets tried, when in equilibrium with 80 % R.H. at 25° C., has been assessed roughly by noting the physical changes in them and the behaviour of flea larvae when fed on them. It was observed that whenever the water content of a food was so low that it just permitted flea larvae to grow, the food particles adhered to the larvae and the pupae, and the fully grown defaecated larvae failed to spin cocoons, perhaps because they could not afford to lose water through secretion of silken threads for spinning cocoons (Sharif, 1948). Appreciable increase in volume of a dry diet at 80 % R.H. denotes its high water content. Even variation in the colour of diets, especially those that contained blood, indicated different proportions of water. If the colour of the food was dull red, its water content was low; but if it was bright red, the water content was high.

(*a*) *Blood.* Dried horse blood alone was completely unsuccessful as a larval diet for *X. astia* and *X. brasiliensis* (Table 1); most of the larvae died in the first instar, though 3·9 % of them in the former species reached the third instar, and 3 % in the latter formed small naked pupae after 29–42 days, from which no adults emerged. It was also very unsuitable for the larvae of *X. cheopis*, but in this species 3·3 % larvae bred successfully into small but strongly sclerotized adults; most of them died in the second instar. The fact that the average duration of the resting larval and pupal life of this species (Table 2) on blood alone was not statistically different from that on a mixed diet of blood and flour, or blood and yeast, suggests that the slight success in rearing adults was due to a favourable change that occurred in the dried blood on prolonged keeping at 80 % R.H.

Only a few larvae of the three species grew slowly and irregularly on blood alone, which was unsuccessful in bringing about pupation and cocoon formation. A significantly lower proportion of the dead larvae of *X. cheopis* than that of *X. astia* on this food (Table 1) indicates the simpler nutritional requirements of the former species. In *X. brasiliensis* 160 larvae died in different active instars in 13–55 (25·31 ± 0·8319) days, in *X. cheopis* 145 larvae in 13–49 (32·48 ± 0·6965) days and in *X. astia* 178 larvae in 9–58 (31·32 ± 0·9215) days. The fact that only the average period taken by the larvae of *X. brasiliensis* to die on this food was significantly shorter than that taken by the other two species, shows that blood is most unsuitable for the larvae of this flea.

Throughout the exposure of 70 days to 80 % R.H., the blood remained dry, dull red and discrete; it did not swell appreciably, as its moisture content was very low (see Sikes, 1931, p. 244). The blood particles adhered to the larvae in large numbers, especially to the dead ones; this hindered the growth of fungus on the dead larvae, which normally occurs at this humidity.

(*b*) *Wheat flour.* Highly milled wheat flour devoid of bran is deficient if used as the sole diet, as only 27 % of larvae in *X. cheopis*, 42·9 % in *X. brasiliensis* and 20·5 % in *X. astia* were reared into adults, and these after very long intervals (Tables 1, 2). This food gave rather better success with the larvae of *X. brasiliensis*; the average active larval life of this flea was statistically the shortest, though it was significantly longer than that of *X. cheopis* when reared on the mixed diet of blood and yeast.

When larvae are fed on flour, there is a considerably longer active larval life, and a significantly higher mortality rate in the larval stage and lower proportion of cocoons formed in *X. astia* than in the other two species (Tables 1, 2): this might be attributed either to insufficient moisture in the meal in equilibrium with 80 % atmospheric humidity, or to its comparatively low nutritive value for the larvae of this species. The latter alternative appears to be more reasonable, as the fact that some larvae lived a long time and spun cocoons demonstrates the presence of enough moisture in this food at this humidity.

The growth of flea larvae on flour was irregular, as every developmental stage from the first larva to the adult were found after 41 days in *X. cheopis* and *X. brasiliensis*, and from the second larval instar to the adult after 60 days in *X. astia*. There were 10·5 % lagging larvae in *X. cheopis*, 8·2 % in *X. brasiliensis* and 15 % in *X. astia*; they lived for 45–63, 40–55 and 72–91 days respectively, and did not form cocoons or pupae. When flea larvae (Table 2) were nourished on an ideal diet of blood and yeast, all the adult females emerged first, and then 2 days after the males started emerging; but when they were reared on flour alone, the adults of both the sexes emerged indifferently. This fact and a marked disparity in the developmental rate of flea larvae on flour indicate that some favourable change had occurred in it, which permitted successful breeding of some of the larvae. The only appreciable change observed was that the dead larvae and flour had slight fungous growth. It is suggested that highly milled wheat flour without bran, by itself, is an insufficient diet for flea larvae, and that association of micro-organisms, such as fungi or perhaps yeast or bacteria, with it was responsible for the successful growth of some of them.

only 1 g. was used; for a mixed diet ½ g. of each of the constituents was thoroughly mixed before the addition of the sand. In these experiments Merck's 'Yeast medicinal dry powder', dried horse blood and highly milled wheat flour devoid of bran were used.

Every possible precaution was taken to avoid any other organic substance coming in contact either with sand or food. Sable's hair brushes and Petri dishes, utilized for examination of the larvae, were always thoroughly washed with soap and water. Brushes were sterilized with absolute alcohol, and Petri dishes were flamed. In no case was the same brush or Petri dish used for two different diets.

Only completely unfed and recently hatched larvae less than 24 hr. old were employed. The larvae were reared in specimen tubes which were placed in a desiccator, containing an atmosphere of 80 % relative humidity (R.H.) controlled by a mixture of extra pure sulphuric acid (Merck) and water in a proportion given by Buxton & Mellanby (1934, p. 174). The desiccator was placed in a dark cupboard in an air-conditioned room maintained at 25° C. (77° F.) ± 1° C. All the experiments were conducted under parallel conditions.

By breeding the three Indian rat-fleas on different diets but under otherwise similar conditions, I have attempted to isolate the nutritional factors and to study their effect statistically. For assessing the nutritive values of the diets the criteria adopted were: (1) the duration of the active larval life and that of the combined larval and pupal life for both sexes, (2) mortality rate in the larval stage, (3) proportion of cocoon formation or pupation, (4) proportion of success in rearing of adults, (5) regularity or irregularity in emergence of adults of both sexes, and (6) variation in the size of adults. Most of these features were statistically evaluated, and were subjected to suitable tests of significance based on the formulae given by Fisher (1941) and Fisher & Yates (1943). In order to ensure the accuracy of results, the experiments of each type were repeated for the number of times entered in the column marked 'Experiments tried'. The results of all the experiments of a type were poolod. The means given are weighted averages. The tests of significance used were the $t$ and $\chi^2$, using 'Yates' correction for continuity' except when the numbers were too few and the exact method of $\chi^2$ was used. When tested in pairs for significance, a result of comparison which is not statistically different is denoted by the sign of $-$, that which is significant at 5 % level is indicated by $+$, and that at 1 % level by $\times$. The signs in each column of the tables indicate the level of significance between a particular value, against which a sign is inserted, and the one higher in the column with which it is connected by an arrow.

Undoubtedly, the 'best criterion for assessing the suitability of a diet is the length of larval life, *i.e.* the time from hatching to pupation' (Fraenkel & Blewett, 1943*b*, p. 459); but in fleas whose larvae spin cocoons, it is very difficult to ascertain the exact duration of the complete larval stage. Consequently, only the active larval life up to the time of cocoon formation has been taken into consideration. In cases where the larvae formed naked pupae, the duration of larval life up to the resting larval stage is assessed, as the time taken for cocoon formation approximates to that.

## III. HISTORICAL SURVEY

Since the time of Leewenhoeck (1683, p. 78), many workers have tried to rear flea larvae under experimental conditions. The diets used by them have been mentioned elsewhere (Sharif, 1937, pp. 226–7). From the results of Bacot (1914, pp. 513–33), Webster (1930, pp. 398–403) and Sikes (1931, pp. 246–8), it appears that the methods employed by them in rearing flea larvae were not very successful, as a fairly high and variable mortality occurred in their experiments. In 1937 I described a standardized food for flea larvae, consisting of dried horse blood and yeast, which has been very successful, as almost 100 % success was obtained in rearing fleas from larvae to adults. Further, this food has the advantage that its quantity and quality can be gauged exactly. On consideration of my findings, Buxton (1937, p. 12) suggested that yeast 'presumably supplies accessory food factors, one may suppose that under natural conditions micro-organisms serving the same purpose occur in fragments of bedding or of rat's dung'.

In view of the different role of species of flea in the epidemiology of plague (Hirst, 1923, p. 817), the question of the distribution of three species of *Xenopsylla* Glinkiewicz in India has gained great importance. Consequently, many workers (see, for instance, Cragg, 1921, 1923; Hirst, 1926, 1927*a*, *b*, 1933; Sharif, 1930) have given detailed records of their distribution in India, Burma and Ceylon. Buxton (1941) has mapped their distribution in the world. In spite of these attempts the irregular distribution of these rat-fleas still defies reasonable analysis.

## IV. EFFECTS OF DIFFERENT DIETS ON THE DEVELOPMENT OF THE LARVAE OF THE THREE INDIAN RAT-FLEAS

In order to determine the comparative nutritional requirements of the larvae of the three Indian rat-fleas, their recently hatched and unfed larvae were reared on (*a*) blood alone, (*b*) highly milled wheat flour devoid of bran, and mixed diets in equal parts of (*c*) blood and wheat flour, and of (*d*) blood and yeast. The differences in their development on these diets

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# NUTRITIONAL REQUIREMENTS OF FLEA LARVAE, AND THEIR BEARING ON THE SPECIFIC DISTRIBUTION AND HOST PREFERENCES OF THE THREE INDIAN SPECIES OF *XENOPSYLLA* (SIPHONAPTERA)

BY M. SHARIF, D.SC. (PANJAB), PH.D. (CANTAB.), F.N.I., B.M.S.(I).
*Assistant Director in Charge of Department of Entomology,*
*Haffkine Institute, Parel, Bombay (India)*





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## I. INTRODUCTION

It is now known that stored agricultural products (see, for instance, Buxton, 1932, p. 291; Hirst, 1927*a*, p. 405), such as cereals, pulses, fodder, cotton, etc., serve as convenient vehicles for the transport of rats and their fleas from one place to another even at a great distance. The possibility of transport of *Xenopsylla cheopis* (Rothschild) by ships absolutely free from rats was hinted at by Hirst (pp. 318, 420). The Advisory Committee (1908, p. 255) suggested that the larvae of fleas, 'since they can feed upon almost any kind of organic rubbish, and pupae, which require no food, could be carried considerable distances in merchandise, *i.e.* for periods as long as one or two months'. The Committee actually found (p. 241) a number of the larvae of this rat-flea 'in the sacking' in the neighbourhood of a 'nest made by *M. rattus* on a grain bag'. In view of the fact that the 'factors governing transference of the species of fleas from place to place are still imperfectly understood' (Hirst, 1933, p. 96), it was considered necessary to ascertain whether the larvae of *X. cheopis*, *X. brasiliensis* (Baker) and *X. astia* Rothschild can breed successfully on the flour of cereals alone. As the stored grains, especially those of wheat, rice, millets, barley, etc., are attacked by insect pests, such as the larvae and the adults of beetles, *Sitophilus granarius* (Linnaeus), *S. oryza* (Linnaeus), *Tribolium confusum* Duval, *T. ferrugineum* (Fabricius), *Oryzaephilus surinamensis* (Linnaeus), *Rhizopertha dominica* (Fabricius) and *Sitodrepa panicea* (Linnaeus), the larvae of moths, *Sitotroga cerealella* (Olivier) and *Ephestia kuehniella* Zeller, etc., small quantities of the excrement and detritus that they produce are always present. Eggs are laid by fleas indiscriminately in the stored products, when rats infested with fleas visit them. Larvae hatched from such eggs possibly may have no food supply other than the flour dust (Bacot, 1914, p. 513; Hirst, 1927*a*, pp. 397, 404), as owing to the frequent shifting of the stored products, the larvae of fleas are usually forced to live in an environment, in which there is little chance of the presence of flea and rat faeces.

The findings presented here are based on experimental work done in the laboratory and on about 3 years' field experience gained in an inquiry into the recrudescence of plague in the districts of Sholapur and Dharwar in the Bombay Province. The observations made provide a reasonable explanation for the host preferences and the irregular and patchy distribution of the three species of rat-fleas in India. An account of the ecological conditions governing the burrows and nesting conditions of both wild and domestic rodents in these districts will be published later; but a few of the observations bearing on the present problem have been incorporated in this paper.

## II. METHODS AND TECHNIQUE

The methods employed for conducting the experiments were similar to those described in an earlier communication (Sharif, 1937, p. 225). The different diets used were given in a finely powdered form thoroughly mixed with 5 g. of ignited and acid washed fine quartz sand. In the case of a simple diet

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but it must be pointed out that exclusive attention to the control of fleas and rodents without adequate knowledge of their ecology may lead to waste of effort, as past experience clearly points out. This can be remedied by subsidizing research on the ecology of fleas and rodents in institutes interested in this type of work.

Pakistan cannot afford to neglect research on fleas and other disease-carrying insects. It must have a research institute with an active band of workers so as to make valuable contributions, and earn its rightful place amongst the progressive nations of the world.

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The Central African endemic centre is said to have been established as late as 1897 (Koch and Zupita, 1898) ; but according to some workers it is certainly of a very old standing, and may be the original home of plague. Payne (1907), however, considers it only a colony of the Asian endemic centre. The remaining centres, *i.e.*, South African, Californian and South American, are fundamentally different from the Central Asian Centre, because in them wild rodents were not primarily involved ; but received infection from domestic rats during the present pandemic only.

It appears that many of the plague endemic centres have escaped detection, and further work is required to delimit precisely all the endemic centres in the world. The conditions governing these endemic centres have been little studied. Sharif (1951) studied conditions prevailing in an endemic centre in the Western Ghats in the Bombay Province for about eight years. In this Province wild rodents do not play any part in the perpetuation of plague ; only the domestic rats are involved.

According to Sharif (1951), in the Bombay Province two distinct types of plague epizootics exist. In the warm, low tablelands and plains, the infection is often severe, leading to a very heavy mortality among rats, which results in disappearance of the disease within a short time. The re-occurrence of plague in them is due to fresh importation. In the cooler regions comprising the watershed of the Western Ghats, the infection is slow-spreading and persists for a long time, owing to lower rat mortality due to the retarding effect of the comparatively low temperature on the increas of flease and of plague bacilli in them. The recrudescence of plague in many places of these areas is the result of carry-over, which are considered to constitute an endemic plague centre. Plague often radiates from an endemic centre. The necessary factors gov erning such a centre appear to be moderately damp and cool climatic conditions for a greater part of the year, which keep the soil in the rat-burrows moderately moist. These conditions permit continuous, good breeding of rat-fleas in burrows and their wandering away from them.

Plague endemic centres are found at an elevation of 1,000 to 2,000 feet in the temperate regions and 2,000 to 4,000 feet in the tropical ones (Hirst, 1929) having an annual rainfall of 20—40 inches, encountered in the submontane regions of the Himalayas and in the gradual slopes of mountains, such as the watersheds of the lower mountain ranges in central and peninsular India, respectively. The disease does not occur in excessively damp areas such as East Pakistan and Assam, and excessively dry areas like the deserts have never shown endemicity of plague. The complete absence of plague from extremely wet areas is due to the harmful effect of excessive moisture in combination with a soil rich in organic material on the breeding of rat-fleas (Sharif, 1949).

Plague is a migratory disease, and even in an endemic centre it is never confined to any one place, though it persists in certain adjacent areas having similar climatic conditions. Such areas have been defined by Sharif (1951), in the eastern gradual slopes of the Western Ghats in Dharwar, Belgaum, Satara and Poona Districts.

From the past records of plague incidence in the Indo-Pakistan Subcontinent, Sharif (1951), has delimited seven endemic centres in the subcontinent. Three of them are located in the submontane plains of the Himalayas. Of the others, three are found in the water-sheds of the mountain ranges of Southern India and one in those of Central India.

Because of the absence of plague in the human population of West Pakistan in recent years, the people of Pakistan should not be lulled into a sense of security, for any such security may easily prove a false one. Plague all through history has had periods of quiescence and recrudescence. No one can tell when the disease will strike again and where. A part of one of the sub-Himalayan endemic centres is in the Punjab.

## VII. CONCLUSION

Commendable progress has been made in our knowledge of fleas during the last fifty years ; but need for further expansion of our knowledge of these dangerous insects will be readily admitted. Fleas have been considered remarkable insects for the difficulties they present in understanding them, and for dangerous diseases like plague and typhus which they transmit. Our time appears especially to demand a well-planned study of these insects. A knowledge of them is of the utmost importance for defence in the bacterial warfare. Fleas are said to have been used once in starting plague during the last war.

The morphology of fleas is a great stumbling block in our way to understand their various aspects. It is a subject which can be studied effectively only in institutions interested in pure research and by entomologists well versed in insect morphology.

The taxonomy of fleas needs greater efforts than have been made hitherto. It is hoped that the recent attempt by Dr. K. Jordan and his colleagues at the Tring Museum, Herts (England) to bring workers on fleas closer by keeping them in touch with one another's activity would lead to their working as a team to put the classification of fleas on a proper footing. The house of Rothschilds has already made a valuable contribution by building up the richest collection of fleas in the world. It is hoped that further help would be forthcoming to prepare a greatly needed monograph on the fleas of the world.

The attempt by the World Health Organization to combat flea-borne diseases like typhus and plague as a long-term policy is a step in the right direction

ventriculus of an infected flea that they blocked the passage, so that blood could not enter the stomach, and that, in the attempts of such a flea to feed, blood carrying organisms were regurgitated and injected back into the wound.

Hirst has (1925) observed that the vector efficiency of fleas varies according to the species, and that *X. cheopis* is the most efficient, which partly explains the patchy distribution of plague in areas having similar climatic conditions. Among the important vectors of plague (see Simmons and Hayes, 1948) are *X. cheopis* and *N. fasciatus* in places where domestic rats play part in plague, *Diamanus montanus* (Baker) and *Hoplopsyllus anomalus* (Baker) in the western part of the United States of America, *N. silantiewi* (Wagner) and *N. tesquorum* (Wagner) in Mongolia, *Rhopalopsyllus cavicola* in Argentina and Ecuador, *X. eridos* Rothschild, *Dinopsyllus lypusus* Jordan and Rothschild and *Chiastopsyllus rossi* (Waterston) in South Africa, *X. brasiliensis* in Uganda, Kenya and Nigeria and *P. irritans* in several parts of the world.

Eskey and Haas (1939) determined the infectibility and infectiousness of 31 species of rodent fleas, five of which are found in the Indo-Pakistan Subcontinent. All fleas became infected ; most of them continued to be so throughout their life ; but 4 per cent of *X. cheopis* and 12—19 per cent of the other species became purified or uninfected. Only blocked fleas belonging to 15 species transmitted plague. In *X. cheopis* the masses of organisms are first formed in the proventriculus, but in most other fleas they are first formed in the stomach, and produce blockage by a secondary invasion of the proventriculus ; consequently, the blockage occurs much earlier in *X. cheopis* than in other fleas. It is for this reason this species is considered the vector *par excellence*.

Normal fleas seldom feed longer than 4 minutes at a time, and would hardly attempt to feed more than once in 24 to 72 hours. Blocked fleas, however, feed as often as every hour or two, remaining longer at one place. Extrinsic incubation period of the infection varied from 5 to 130 days, being 5—31 days in *X. cheopis*, and it was influenced by the temperature, being longer at a lower temperature. The average length of life of fleas after they transmitted plague was only 3.2 days. Fleas of many species may harbour plague organisms without ill effects and lived for 1 to 3 months ; a few even lived for over 5 months ; but *X. cheopis* died in the shortest time after infection, being 17 days at 18.9°C. and 12 days at 22.2°C.

The factors which determine the transmitting power of a particular species are the infection potential, vector potential, transmission potential, extrinsic incubation, life span of the flea both when infected and uninfected, feeding habits and other ectoparasite relationships. Wheeler and Douglas (1945) developed a simple standardized method for ascertaining the vector efficiency

of a flea species by calculating the product of the numerical values of its infection, vector and transmission potentials : more simply, the average number of transmissions by an individual of the species. According to them the vector efficiency of *X. cheopis* is only inferior to that of *D. montanus*, a wild rodent flea of the United States of America.

### (c) Spread of Plague and Endemic Centres

Besides the earlier doubtful records of plague outbreaks, three great pandemics of plague have overrun the world. The first pandemic, the "Justinian plague", which originated from Pelusium in 542 A.D., was responsible for 100 million deaths, and carried off half the population of the Roman Empire. The second pandemic which started in Asia reached its zenith in the fourteenth century, spreading all over the old world. Owing to pneumonic complications it was called "Black Death" in Europe, where it killed about 25 million people, *i.e.*, about one-quarter of its population. The third or present pandemic started from the Yunan plateau in 1893, and within a short time nearly every country became involved. In the Indo-Pakistan subcontinent alone it has killed over 12 million people in about fifty years. Recently, Devignat (1951) has shown that these three pandemics were caused by three different strains of *P. pestis* ; the first one was due to var. *antiqua*, second one to var. *mediaevalis* and third one to var. *orientalis*.

Whenever a pandemic wave of plague recedes from a country, endemic foci comparable to stagnant pools left behind by the lowering tide, exist in moderately cool and damp regions, which continue to serve as perpetual sources for the dissemination of plague. Such endemic foci were left by the second pandemic in the Near East, and by the third one in India and some other countries. These radiate plague to neighbouring areas with a secular tendency.

The question of ancestral home of plague has attracted the attention of many workers (see Wu Lien-Teh *et al.*, 1936), and some of them suggest that the Central Asian plateaux are the original home of plague, for the simple reason that plague foci in them belong not only to the past, but have remained impaired up to the present time. Even the European epidemics have been traced back to them. Five plague endemic centres have usually been recognized in the world ; Central Asian, Central African, South African, Californian and South American.

The Central Asian endemic centre is the oldest in which wild rodents like tarabagan and marmot species are also involved. Wu Lien-Teh (1934) opines that the whole of this vast area with its profuse wild rodent population "might be compared with a heap of embers, where plague smoulders continuously and from which sparks of infection may dart out now and then in various directions".

Wu Lien-Teh, Chun, Pollitzer and Wu, 1936), which are considered abundant in certain seasons of a year and scarce in others. Consequently, a regular alternation between the plague seasons and off-seasons occurs. This is not borne out by the studies of Sharif and Narasimham (1942, 1945). It is not so much the seasonal fluctuations in the flea population that control the propagation of plague, but the behaviour of adult fleas towards climatic conditions. During a plague season a large number of fleas accompany rats during their movements and are thus scattered at random, which helps in the spread of plague; moreover they can remain for a longer time on the human body and in the personal effects during the plague season and thus cause severe epidemics. Whilst during the off-season very few fleas accompany rats and are scattered, and they cannot remain on human body, even when a large number of them may be present in rat burrows. This results in retardation or inhibition of the propagation of plague, and the infection during off-season at certain favourable places pursues the course of a slow subterranean enzootic from burrow to burrow. Evidently, the behaviour of adult fleas plays an important part in tiding over the off-season. Many workers (see Bacot, 1915; Eskey and Haas, 1939) have shown that infected fleas can live for several months on their host without transmitting the disease. These two factors affecting fleas play the most important part in carry-over of plague from one season to another.

It is said that wild rodents like tarabagans, marmots, etc. (Wu Lien-Teh, *et al.*, 1936), when infected towards autumn, may undergo normal hibernation harbouring plague bacilli at or near the site of entry, and on awakening in spring this latent infection becomes active and leads to generalized plague with bacteraemia. But plague predominates in domestic rodents which do not undergo hibernation. Consequently, kindling of latent infection in nature cannot play any part in tiding over the off-season. It may, however, play some part in sylvatic plague in cold countries.

There are a number of factors in nature, which operate against the wide dispersal of plague. There is no active migration in the case of domestic rats. The chances of their passive migration are comparatively few. Domestic rats can be easily carried from one place to another through ships or even small boats, and epizootics have been detected in them; but rarely by means of transport on land. The chances of an infected flea being carried from place to place along with merchandise and even on man and his personal effects are many. Fleas play far more important part in both retaining the infection and in disseminating it than rats. The plague bacilli can survive for a much longer time within the body of flea than is possible within that of the rat. When once they

enter the body of a rat, they either kill the rat when susceptible, and thus get destroyed themselves or get exterminated in the body of an immune rat. Evidently, the survival of plague organisms for a long time is only possible in the body of the rat-flea, and rats only provide facilities for maintaining their flourishing culture. Thus the flea is both a transmitter and a preserver of plague infection, as pointed out by Golov and Ioff (1927) and Prince and Wayson (1947).

### (b) Mechanism of Transmission

Some blood-sucking arthropods like bed-bugs and rodent lice, ticks and mites, etc. (see Wu Lien-Teh *et. al.*, 1936) are known to harbour plague bacilli for a fairly long time ; but so far there is no conclusive evidence to show that any insect, except some fleas, is of any importance in the natural transmission of plague. Several methods of transmission were investigated by the Advisory Committee (1906*a*, 1907*a*), of which the below-mentioned four methods by fleas were reinvestigated by subsequent workers.

(*1*) *Ingestion of infected fleas by animals.*—Most rodents scratch their body with the teeth ; thus they accidentally eat or kill some of the infected fleas, which affords an opportunity for the entry of plague organisms through the abraded surface of their digestive tract. According to this mode there is a chance for some non-flea transmission.

(*2*) *Mechanical infection.*—Some workers (see Swellengrebel, 1913 ; Simmons and Hayes, 1948) claim that plague transmission by fleas is purely a mechanical process, and is effected by plague bacilli present on the proboscis of the infected fleas.

(*3*) *Faecal infection* is produced by the infested animal scratching or rubbing faeces of the infected fleas into the irritable wounds made by the proboscis of the fleas. This method of transmission was first suggested by Simond (1898), and it was supported by the Advisory Committee. Bacot and Martin (1914), however, showed that plague bacilli lose their virulence in the stomach of a flea, and only a few of them are passed in the faeces which soon dry up. Eskey and Haas (1939) have demonstrated that it is not possible to infect guineapigs by rubbing into the scarified skin both fresh or dry faeces of infected fleas. They, however, maintain that plague organisms can survive in dried faeces for five weeks at the room temperature.

The above-mentioned three methods of plague transmission should lead us to believe that every flea is equally an efficient vector ; but our knowledge of epizootics and epidemics of plague is definitely against it.

(*4*) *Regurgitation infection.*—Bacot and Martin (1914) showed that plague bacilli multiplied in such large masses in the interstices of the spines in the pro-

The larval food appears to be an important factor that governs the distributions and host preferences of different species of fleas. The larvae of *X. astia* need the most nutritive diet. This species flourishes, if a rich larval food is present in a rodent burrow, as in the burrows of *Tatera indica* and *Bandicota malabarica* (Shaw), and even in those of the domestic rats in certain regions, where their nesting conditions provide rich food for the flea larvae. On the other hand, the nutritional requirements of the larvae of *X. cheopis* and *X. brasiliensis* are simple; thus they prosper readily in a burrow of the domestic rat, even where the nutritive value of the larval food is very low, as is the case in the plateaux of peninsular India, where jowari, bajri and cotton are the main agricultural products. As the temperature tolerance of *X. brasiliensis* (see page 17) is the lowest, this species is confined to some of the cooler regions.

The irregular distribution of the three species of rat-fleas in the Indo-Pakistan subcontinent may be related to differences in the nutritional value of the varied organic substances found in rat burrows in different places. The fact that the distribution of *X. cheopis* and *X. brasiliensis* is wider than that of *X. astia* is attributed to the ability of their larvae to grow better on flour alone; this possibly enables them to survive transport in grain, even without rats, to places far from their original home.

## VI. RÔLE OF FLEAS IN PLAGUE

Plague is primarily a disease of rodents, and man has become an incidental victim. The earliest recognition of the causal connection between plague epizootics and epidemics is probably indicated by the offerings, made by Philistines when restoring the Ark they robbed from Cannan, which consisted of golden images of mice and of emerods or bubos [1 Samuel, v & vi]. Plague came to be associated with man and merchandise in transit from plague infected areas long ago, and from 1374 onwards measures of isolation and quarantine were increasingly enforced for the control of the disease. The discovery of the plague bacillus by Yersin and Kitasato in 1894 at Hong-Kong, was soon followed by a hypothesis that fleas transmit plague organisms from rat to rat and from rat to man by Ogata (1897), Simond (1898), Gauthier and Raybaud (1903) and Verjbitski (1904) proved experimentally that plague could be transmitted from rat to rat by fleas. Liston (1905) and the Advisory Committee (1906*a* 1907*a*) definitely established the transmission of plague by the rat-flea.

From an epidemiological viewpoint Jorge (1928) distinguished between the pandemic plague found in the domestic rodents, taking a very heavy toll of human life all over the world, and the sylvatic plague found in the wild rodents,

only dangerous to man when he approaches the endemic areas populated by wild rodents. Sylvatic plague has been reported from Transbaikalia, Mongolia, South-Eastern Russia, South Africa and the Western parts of the United States of America. Plague at present is predominantly a disease of domestic rats, although originally it might have been acquired from wild rodents in the course of evolution, when the association of rodents with human dwellings occurred. The study of sylvatic plague will naturally lead to proper understanding of the disease.

An active focus of sylvatic plague exists in the western parts of U.S.A., and plague has been reported in the wild rodents of 138 counties of fifteen western states (Link, 1951). Since 1934 extensive investigations are being carried out under the supervision of the Sylvatic Plague Committee, and the reports of the work done are published from time to time. Much has been added to our knowledge of plague by these investigations (see Eskey and Haas, 1940). Garnham (1949, p. 272) gives an account of the wild-rodent plague, and according to him this type of plague "seems to have been accompanied by no large-scale human epidemics". History of the sylvatic plague in the South Africa is given by Mitchell (1927) and Davis (1948).

### (a) Preservation of the Plague Organism in Fleas

Plague is an acute infectious disease, and its three important factors are the causative organism, *Pasteurella pestis* (Yersin), the rodent hosts and the rodent fleas, representing respectively the fountain head, the perpetuating force and the motive power in an unholy trinity. The plague epizootics and epidemics depend on the interplay of these three factors in relation to the climatic conditions. The bubonic plague is communicable as long as septicaemia exists in the rodent host and a suitable flea vector is present.

The aetiological rôle of rodents has been definitely established; but a complete harmony between the plague organism and any of its hosts has not been achieved. The so-called cases of chronic plague amongst rodents have been shown by the Advisory Committee (1906*c*, 1910*a*) to be stages of progressive recovery or "resolving plague" with entrenched infection at a site without any bacteraemia. The rodents suffering from chronic plague infection naturally will develop concomitant immunity, which thus cannot contribute to the propagation of the disease.

The fact that epizootics are usually limited in extent and slow in their spread plays a very important part in the maintenance of plague amongst the prolific breeding rodents. The factor responsible for the irregular distribution of plague in time is often considered to be seasonal incidence of fleas (see

More detailed and precise work on the effects of temperature and humidity on oviposition and egg-hatching, especially in the case of rat-fleas, is highly desirable, as their eggs are carried in grain merchandize from place to place, and the only method of killing them is by exposing them to fatal temperatures.

### (c) Effects of Temperature and Humidity on Larvae and Pupae

Our knowledge of the bionomics of rat-fleas remained imperfect until very recently. The larval diets used by several workers (see Sharif, 1949) for rearing fleas had a poor and varied nutritive value, as is borne out by high and variable mortality rates in their experiments. The food factor might have influenced the results which are attributed to climatic conditions. For ascertaining the effects of variations in temperature and humidity on the growth rate of flea larvae and pupae, Sharif kept all other factors such as food, light, soil and atmospheric pressure uniform in his experiments. Temperature influences the developmental rate of flea larvae and pupae more than himidity. The effective temperature range for the larvae varies according to the species, being 12°—35.5°C. in *X. brasiliensis*, 12°—36.5°C. in *X. cheopis* and 13.5°—38°C. in *X. astia*. The medial temperatures for their development varied from 17°—29°C. in the first pecies, 17°—30°C. in the second and 23°—33.5°C. in the third. The effective humidity range was much narrower in *X. astia* and slightly wider in *X. cheopis* than in *X. brasiliensis*. The fact that the water balance of the larvæ of three species could only be maintained at 50 per cent and higher relative humidities and their developmental rate was not affected materially at a fairly wide range of favourable humidities suggests that the moisture content of the debris affects directly the rearing of fleas and not the burrow humidity above. For the normal breeding of flea larvae the presence of soil or débris is very necessary.

Relative humidities higher than 90 per cent by themselves have no deterring effect on the development of the early stages of fleas ; but their effect on flea breeding was mainly controlled by the amount of the organic material present in the sand or débris. When the sand was rich in organic material, death of larvae and pupae occurred due to suffocation caused by the formation of a crust and compact mass and by the sogginess of food and sand mixture ; but it could be avoided by disturbing the mixture so as to allow free access of air to these stages. Sharif (1949) attributes the paucity of fleas observed in the burrows of *Millardia meltada* (Gray) and *Gunomys kok* (Gray) to the presence of excessive moisture and débris rich in organic material, abundance of fleas in those of *Tatera indica* (Hardwicke) to the absence of the first factor alone, and moderate flea infestation generally found in those of domestic rats to the absence of both these factors.

Sharif (1948*b*) proved that excessive loss of water in the flea larva through its defecation and excretion as the result of absence of rectal glands, through a profuse evaporation from the surface on account of its being a soil inhabitant, and from its tracheal system owing to the absence of an efficient closing apparatus of the spiracles, is compensated by the absorption of water with the food and through cuticle, and by the utilization of the metabolic water.

### (d) Nutritional Requirements of Larvae

Blood is considered as an integral part of the larval food for most fleas; but Sharif (1937*a*, 1948*a*) showed that sterile dried blood alone was not sufficient for the successful development of the rat-flea larvae, and so was yeast alone. The mixture of the two, however, gave almost hundred per cent success in the rearing of fleas. As yeast possesses growth-promoting substances, the vitamins of the B group, it is considered that the native proteins of blood and B vitamins form an ideal food for flea larvae. Like some other insect larvae the source of these vitamins (see Fraenkel and Blewett, 1943; Hobson, 1933, 1935) is micro-organisms like bacteria, fungi, etc., which synthesize them in the food. Possibly the presence of plague bacilli in the faeces of adult fleas which their larvae often eat help to explain, in part, the great number of fleas which have been observed on rats in plague-infected houses (see Hirst, 1926).

The comparative nutritive value of dried horse blood, highly milled wheat flour devoid of bran, mixed diets of blood and wheat flour and of blood and yeast for the larvae of *X. cheopis X. brasiliensis* and *X. astia* was ascertained by Sharif (1948*a*). The growth of their larvae on wheat flour alone was erratic; only partial success was obtained, and the adults emerged after long and irregular intervals owing to the association of micro-organisms, possibly fungi, with this food. A mixture of blood and wheat flour accelerated their larval development; but it was not as a satisfactory larval diet as blood and yeast, the control diet. Significant differences in the nutritional requirements of the larvae of three species were observed. Advantage of these differences was taken to account for the specific distribution and host preferences of these species of rat-fleas in the Indo-Pakistan subcontinent.

Many species of fleas have become highly specialized not merely in regard to the blood of a particular host, but as to its nesting conditions. The conditions in the burrow make a great difference to larval nutrition and therefore to the absence, presence or abundance of fleas. The examination of about 160,000 fleas of wild and domestic rodents of the Barsi and Dharwar talukas for about three years, and the study of their burrow conditions, have enabled to ascertain some factors that control the irregular distribution of the three species of rat-fleas, which has a great bearing on the spread of plague.

The factors that can possibly control the variations in the population of fleas are food, temperature, humidity, light, atmospheric pressure and the nature of the soil. It is very essential to evaluate the effects of these factors on flea populations individually at first and then collectively. Quantitative work of the type done by Buxton (1938, 1948), Leeson (1932, 1936), Sharif (1937*a*, 1948*a* & *b*, 1949), Smith (1951) and Edney (1945, 1947*a* & *b*) is highly desirable.

### (a) The Adult

The ecology of the adult fleas has not received so much attention that it merits, owing to the important rôle they play in causing two of the most dreaded diseases of mankind, plague and typhus. As to their reaction to the environmental conditions we know very little. According to Chick and Martin (1911), *X. cheopis* and *N. fasciatus*, the rat-fleas, "when hungry, readily bite man". Hirst (1927*a*, p. 258) made observation on the biting propensity of the rat-fleas on man and rat, and found that "*X. cheopis* bites man somewhat more readily than *X. astia*". Better controlled experiments on the behaviour of adult fleas towards different climatic conditions and their biting habits are required, as from the standpoint of plague control it is the psychology of fleas that matters.

(1) *Longevity of unfed fleas.*—As the rat-fleas are known to be carried apart from their hosts in grain merchandise, personal effects, etc., their longevity in the unfed state is of a great interest from the plague viewpoint. Bacot (1914) found that unfed fleas could live many days, a few specimens of *P. irritans* survived for 125 days, of *N. fasciatus* for 95 days and of *X. cheopis* for 38 days at 7.2°—10°C. with nearly saturated air : but at a higher temperature of 26·7°C. or above with a humidity of 60 per cent or less they hardly lived 10 days.

Earlier workers (Advisory Committee, 1908, 1912 ; Bacot, 1914 ; Hirst, 1927*a*) have emphasized that high temperature and dryness, particularly the latter, shorten the survival duration of rat-fleas. Leeson (1932, 1936) exposed large numbers of adult *X. cheopis* of known age, some unfed, others fed once, and others lived with a mouse one week to controlled temperatures and humidities without any further feeding. Their survival duration was determined mainly by temperature, being longer at lower temperature, and the effect of humidity, though definite, was comparatively slight. Only at lower effective temperature fleas lived longer at a higher humidity. He established that survival of fleas was not proportional to saturation deficiency, as was shown by Bacot and Martin (1924), Mellanby (1934) and Wigglesworth (1932, 1935), also have shown that the adult flea is nearly in-

different to humidity, even to a low humidity with high temperature. Thus the adult flea as opposed to its larva is capable of withstanding effect of low humidity ; this according to Buxton (1938) is due to the adult being well protected against heavy loss of water by the presence of an efficient closing mechanism of the spiracle and rectal glands, which is not the case in the larva.

(2) *Longevity of the feeding adult fleas.*—Bacot (1914) observed that *P. irritans* lived for more than 513 days, *N. fasciatus* for 106 days and *X. cheopis* for 100 days, when fed on man. Unfortunately, Bacot kept these fleas at a room temperature and humidity of Loughton in England, where the winter temperature is very low ; possibly the fleas were under the effect of cold stupor, as Bacot's other experiments (Table LV, p, 627) kept at comparatively better controlled temperatures show much shorter survival duration. According to Webster and Chitre (1930*a*), males and females of *X. cheopis*, when entirely maintained on human blood, survived for 63 and 162 days respectively at Bombay. Tiflov and Ioff (1932) in Russia were able to prolong the life of the suslik flea, feeding only once every 1—2 months, for about five years.

Continually feeding adult fleas are even much less influenced by the humidity factor, as they can feed sufficiently to restore any loss of water which a low humidity would cause (Buxton, 1938). It would be of a great importance to ascertain the longevity of rat-fleas at different combinations of temperature and humidity. Furthermore, it would be necessary to determine the threshold of activity of rat-fleas, for exceptionally long life below 10°C. appears to be due to cold stupor. In this connection test-tube method of feeding fleas will be very helpful, as the fleas are liable to be killed by experimental mice.

**(b) Oviposition and Egg-hatching**

We know very little about the precise conditions governing oviposition and egg-hatching in fleas, in spite of the efforts of the Advisory Committee (1908, 1912), Bacot (1914), Hirst (1927*a*), Webster (1930), and Hopkins (1935) ; these workers only ascertained the effects of a few not properly controlled temperatures and humidities on them. A flea lays eggs in batches of less than 10 over a considerable period of time, punctuated by blood meals which are necessary for their development. The hatching of eggs usually occur after 2 to 10 days. According to Bacot, egg laying was adversely affected by the low temperatures and humidities, but in some species fertility increased at a low humidity, and 4.9°C. proved fatal to eggs of *X. cheopis* and *P. irritans* but not to those of *N. fasciatus*. Webster (1930) found that eggs failed to hatch at 37° and 4.4°C.

on the presence or absence respectively of a dorsal sulcus on the head, which divides it into two parts. In actual practice the detection of this groove in some cases is impossible. Jordan (*fide* Hubbard. 1947) and Ewing (1929) are of opinion that there is no basic foundation for the creation of these two sub-orders, and some workers have found the necessity of dividing the fleas directly into families. Unfortunately, there is no general agreement amongst the workers on fleas as to the number and arrangement of their families. Wagner (1939) recognized 10 families and 28 sub-families in addition to many tribes of fleas. A satisfactory and natural classification is as yet to be discovered. To put in the words of Hubbard (1947, p. 47), "Much of the systematic work on fleas is unsatisfactory and many of the keys so far developed are of little value."

The taxonomy of fleas is suffering from the usual disease of creation of too many species by unexperienced workers and too much splitting which may not be necessary : the latter has been regretted by Jordan (1933). A revision of the order in the form of a monograph on the fleas of the world is greatly needed. Jordan (1925) notified once that he was engaged on a "*Monograph of the Siphonaptera*"; but unfortunately nothing material has been done so far. According to Lima and Hathway (1946), there are over 1300 species and sub-species of fleas, and such a large number cannot be managed by any one person, and a team of workers under the guidance of one man will be able to achieve this end. Logically the work of revision of the order should be done at the Tring Museum (England), where the largest collection of fleas in the world is lodged.

## V. ECOLOGY OF FLEAS

A fairly extensive literature exists on the life history and the biology of fleas, and it has been reviewed by Sikes (1930) and Sharif (1937*a*, 1949). Most of it deals with the rat-fleas ; the biology of most other fleas is practically an unexplored field.

*Xenopsylla cheopis*, *X, astia* Rothschild and *X. brasiliensis* (Baker), the rat-fleas of the Indo-Pakistan subcontinent, are experimentally proved vectors of plague (Webster and Chitre, 1930*b*), though their degree of efficiency as vectors may vary. In view of their great medical importance, it is necessary to ascertain the effects of different ecological factors on their reproduction, rate of development and mortality, resultant population, behaviour, distribution in space and time, and host preferences. Though attempts have been made by previous workers (Advisory Committee, 1908, 1912 ; Bacot, 1914) to determine the effects of some of the ecological factors on these fleas, yet,

as pointed out by Hirst (1926) and Buxton (1938), our present knowledge of their bionomics is incomplete.

The primary objects of the ecological studies should be to foresee, if possible, to prevent flea abundance, and to elucidate the factors governing the fluctuations in the flea numbers. The correlation between outbreaks of plague and flea abundance and geographical distribution of these three rat-fleas has been emphasized by many workers (see Advisory Committee, 1910; Cragg, 1921, 1923). In order to assess the natural variability in populations of these insects at a particular time and locality, several workers have made use of the flea count, *i.e.* the number of fleas per rat; this method, as pointed out by Hirst (1926, 1927*a*) and Buxton (1938), is hardly suitable for the purpose.

According to Hirst (1927*b*), the total rat-flea population of a given premises is composed of three components: (1) fleas found on rats, (2) those present in their burrows, and (3) the free wandering fleas. Fleas do not always live on rats; a very large number of them remain in the débris or litter of rat burrows, and a small proportion temporarily visit their hosts to feed. There is not likely to be a fixed ratio between the number of fleas found on rats and those present in their burrows (see Leeson, 1936; Buxton, 1938). Fluctuations in the flea counts of domestic rats are influenced by the state of hunger of the adult fleas and their behaviour towards the climatic conditions at the time when the wandering rats are collected. The micro-climate of rat burrow is often favourable for fleas, and thus most of them remain in it, even when the outside atmospheric conditions are unbearable for them (Buxton, 1932, 1933). In consequence, it is doubtful whether the flea counts of wandering rats have any significance. Obtaining flea census of burrows at different times may give an accurate estimate of the variation in the flea population due to the climatic conditions; but it is beyond practical possibility, as is borne out by the attempts of Davis (1939).

It is, however, suggested that flea counts which have been our only weapon, so far, for assessing the variability of flea populations due to climatic factors have failed us; much time and energy have been wasted on them, and many wild assumptions have been made without having any knowledge of their exact significance. An accurate knowledge of the ecological factors that govern the fluctuations of flea populations will be more useful. This will also enable us to understand the real significance of the flea count, as "the matter is important enough to demand study from a new angle, the experimental, so that we may acquire knowledge of the limitations of this widely used method" (Buxton, 1938, p. 528).

with that of mammals. The remains of the most ancient mammals have been discovered in Asia, and fleas seem to have originated along with them. This is borne out by the fact that there is a similarity between the North American and East Asian fleas that are found on mammals which are considered to have migrated from East Asia into the North-America.

Without the necessary reliable record of the past, the links in the evolutionary chain can only be deductions based mainly on comparative morphology and embryology. Jordan (1950, p. 1) suggests 'a partial reconstruction of the ancestral flea' from what we know of the existing fleas will help ; but comparative morphology can only be helpful if we can distinguish the generalized types of structures from the specialized ones. Unfortunately, fleas as a group are so highly specialized and their morphology so inadequately understood, that many workers have laid stress on features whose very existence is a matter of dispute ; consequently, the homologies of fleas would mock at every attempt.

Spines and excessive hairyness of fleas are adaptive features in accordance with their being ectoparasites of hairy mammals and feathery birds. This would lead to the conclusion that less hairy fleas without spines are more primitive. A detailed morphology of such a flea, especially of *Pariodontis riggenbachi* (Rothschild), will throw some light on the affinities of fleas.

The study of embryology of fleas like their comparative morphology has failed to explain the relationship of fleas with other insects. Kessel (1939, p. 3), who gives a detailed account of the embryology of three species, belonging to three different families of fleas, opines "it is inadvisable for the writer to attempt a phylogenetic application of the present observations until he has personally investigated the embryology of those forms which are suspected of being most closely related to the Siphonaptera". Undoubtedly, comparative embryological observations are valuable in the solution of phylogenetic problems; but it must be taken into cognizance that the embryology of the fleas cannot differ fundamentally from that of the other holometabolous insects. The differential characters of most holometabolous orders are largely developed during the postembryonic life. In order to ascertain the phylogeny of fleas one has to look to their postembryonic development especially during the pupal stage as pointed before (see p. 8).

Fleas are extremely specialized insects owing to their prolonged parasitic association with mammals. They might have been very simple holometabolous insects, probably in the Triassic period, but now they have developed extremely specialized features which have masked their simplicity beyond recognition. Fleas seem to have no close relationship with any of the existing insect orders. Probably they separated from the holometabolic

stock at a very early stage. According to Crampton (1931), fleas alone are entitled to the rank of a superorder, the Pansiphonaptera, which is one of the three superorders into which he has divided all the holometabolous insects. The other two are the Panmecoptera, containing the Neuroptera, Mecoptera, Diptera, Lepidoptera, and Trichoptera, with their fossil allies, and the Pancoleoptera, comprising the Coleoptera, Strepsiptera, and Hymenoptera, with their fossil allies except the Protohymenoptera. His assumption appears to be nearer the truth.

## IV. SYSTEMATICS OF FLEAS

Linnaeus (1758) listed only two species of fleas. This was followed by scattered anatomical and systematic notes on fleas by Bosc (1801), Curtis (1832), Dugès (1832), Westwood (1838), Bouché (1835), Haliday (1856) and others. Kolenati (1863) gave a systematic account of the fleas which he divided into eight genera. Taschenberg (1880) recognized two families and five genera, comprising 33 species. Baker (1904) listed 135 species of fleas then known in the world, which he divided into 5 families ; subsequently, he (1905) arranged them into 8 families. In the beginning of the present century, the discovery that the plague bacillus is transmitted by fleas led to a serious study of their taxonomy. Amongst the workers that have contributed largely to the systematics of fleas, the names of Dampf, Wagner, Oudemans, Rothschild and Jordan deserve to be mentioned. A catalogue of fleas of the world was published by Dalla Torree (1924). Of the numerous papers published by Jordan and Rothschild, two papers (1906, 1908) are of a considerable interest. Wagner published a large number of papers including four extremely valuable catalogues of fleas (1930, 1936*b*, 1938, 1939).

The taxonomy of the North American fleas has received a considerable attention during the last fifteen years ; a number of monographic works by Fox (1940), Ewing and Fox (1943), Hubbard (1947) and Holland (1949) have appeared. Jellison and Good (1942) prepared an "Index to the literature of Siphonaptera of North America". Almeida Cunha (1914*a* and *b*) has described the Brazilian fleas.

Over eighty species have been recorded from the Indo-Pakistan subcontinent, and only a revision of the family Pulicidae was published by Sharif (1930).

The order of fleas, for which three names, *viz.*, Suctoria, Aphaniptera and Siphonaptera are being used, has been divided by Oudemans (1909*a*) into two sub-orders, Integricipita and Fracticipita ; this division is based

based on completely insufficient and defective interpretations of the morphology of fleas themselves but also that of insects in general. During the last fifty years our knowledge of the morphology of insects has advanced considerably, but that of fleas has not kept pace with it. Consequently, fleas still stand isolated among the orders of holometabolous insects, and different attempts to relate them with the other orders have failed for lack of sufficiently convincing evidence.

Martini (1922), who considers fleas having relationship with the Coleoptera, points out many similarities between fleas and the genus *Oxytelus* belonging to the Staphylinoidea ; but these homologies as pointed out by Ewing and Fox (1943, p. 11) "are of a very general nature and doubtless exist between fleas and many other kinds of insects".

Crampton (1931), considers the Trichoptera as ancestors of fleas ; for they have three-segmented labial palpi, and their prothoracic sclerites, cerci and male genitalia and the division of their mid- and hind-coxae into a eucoxa and meron are similar to those of fleas. But Snodgrass (1946, p. 29) points out that the posterior part of coxa of fleas, called by Crampton meron, "has no anatomical identity with the meron of such insects as Mecoptera, Trichoptera, and Lepidoptera" and that the male genitalia of fleas are unique. The true cerci are absent in the fleas as shown by Ewing and Fox (1943). Tillyard (1935, p. 39) attacked Crampton's theory very vehemently for many reasons, and according to him "There is not a shred of evidence in favour of Fleas having been derived from an aquatic ancestral type. Their whole life-history points to their having been derived from an ancestor which possessed a purely terrestrial larva".

For a very long time many entomologists have held the view that fleas are somewhat related to the Diptera. Packard (1894, p. 354) emphasized this relationship greatly, for the "larva of the Siphonaptera apparently presents the nearest approach of any of the insects now existing to the shape of the primitive Diptera", and for many other reasons. Dahl (1898) derives the fleas from a hypothetical stem the *Archiscatopse,* whose other living representatives are the nematocerus genus *Scatopse* and *Phora.* This is really very speculative, even though Ewing and Fox (1943, p. 11) maintain that Dahl's "theory is one of the best proposed, and he has given many data in support of it".

According to Tillyard (1935, p. 33), "the Fleas cannot possibly have been descended from Diptera, for the obvious reason that the Fleas retain a complete metathorax, whereas the Diptera, right from the earliest known types, have this segment greatly reduced and incorporated with large mesothoracic mass, in correlation with loss of the hindwings". Previous to this Crampton (1931)

has also emphasized the importance of this evidence. The discovery of wing buds on the mesothorax of pupae of three genera of fleas by Sharif (1935, 1937*b*) at first sight would suggest the relationships of the fleas with the Diptera ; but according to Snodgrass (1946, p. 20), "Ontogeny does not necessarily repeat the whole ancestral story ; the presence of wing vestiges on the pupal mesothorax may represent in the fleas simply the last stage in the elimination of the organs of flight that accompanied the evolution of the legs into organs for jumping. The hind legs and the metathorax are the parts most highly modified for leaping, so probably the metathoracic wings were the first to be lost, and are not known to be recapitulated in ontogeny. The large size of the metathorax in the fleas argues against the derivation of Siphonaptera from Diptera".

Tillyard (1935, p. 38) considers "the Fleas to be a part of the Panorpoid Complex and that they must have been derived directly from Mecoptera rather than from Diptera". His theory demands that the ancestors of fleas must have possessed short antennae, elongated mandibles, four-segmented maxillary palpi, two-segmented labial palpi, a smooth and leathery body, metathorax not highly reduced, middle and hind coxae with a meron, and a terrestrial larva feeding on animal or vegetable débris, a free pupa either in a cocoon or a primitive earthen cell. He (p. 43) believes that the only possible ancestors that satisfy these conditions are "(a) a small, reduced type of primitive Mecopteron, probably of the Upper Permian family Permochoristidae, or (b) a related form classifiable definitely within the Paratrichoptera". It is, however, difficult to agree with Tillyard, as there are numerous gaps to be bridged over in his theory.

The fleas are unknown in their primitive manifestations ; consequently, their ancestry is wrapped in obscurity. The subject can only be approached by the co-ordination of whatever evidence may be gleaned from three principal courts of appeal, palaeontology, comparative morphology and embryology.

Of these, palaeontology has, so far, remained almost like a closed book. The oldest known fleas found in the Baltic amber belongs to the genus *Palaeopsylla*, which is very similar to the existing species of the same genus (Jordan, 1950). There is, however, an indirect evidence based on the palaeontology of their fundamental hosts, the mammals. According to Holland (1949), fleas originated in a remote geologic past as temporary ectoparasites of archaic small mammals. They are even now predominantly ectoparasites of small mammals, but the transference of a few of their genera or species to birds seems to have occurred at a much later period. Certain fleas have a preference for a particular genus or species of hosts. Fleas belonging to the family Ischnopsyllidae are exclusive parasites of bats. Possibly the origin of fleas have some relation

exclusively formed by genital portions of the ninth and tenth sterna and cannot be considered aedeagus. His earlier definition (Snodgrass, 1935, p. 621) of endophallus, "The inner chamber of the phallus invaginated at the end of aedeagus" does not warrant the use of this term for a structure anterior to the aedeagus. Snodgrass (1946, p. 58) has, however, made certain modifications in the definition of endophallus, which only can be applicable to the structure named by him "inner tube of aedeagus" ; the latter should have been designated aedeagus as has been done by Jordan (1926). The basal apodeme of aedeagus is nothing else but an apodeme of the genital portion of tenth abdominal sternum as is elucidated by Sharif (1945). Undoubtedly, there is a little confusion about the homology of some parts of the male genitalia ; but it can only be cleared by the study of their post-embryonic development, especially during the pupal stage.

### (b) Internal Anatomy of the Adult

Amongst the earlier workers to whom we owe our knowledge of the internal anatomy of the adult flea, the names of Karsten (1864), Landois (1866), Bonnet (1867), Wagner (1889) and Packard (1894) deserve to be mentioned. Lass (1905) mainly devoted his attention to the anatomy and post-embryonic development of the female reproductive organs of the dog-flea. Advisory Committee (1906*b*) described the alimentary canal of *Xenopsylla cheopis* (Rothschild).

Oudemans (1909*b*) and C. Fox (1914) pointed out the systematic value of the spermatheca, and Dampf (1912) described the morphological significance of ductus obturatorius. Cholodkovsky (1914) gave an account of the internal male organs of reproduction and the rectum of the dog-flea.

For the most of what is known to us about the internal anatomy of the adult flea, we are indebted to Patton and Cragg (1913), Patton and Evans (1929) and Minchin (1915). Martini and Burgarth (1923) describe the internal and external anatomy of the female dog-flea with a view to ascertaining the systematic position of fleas.

Pavlovskij (1926) gives an illustrated account of the internal reproductive organs of the males of six species. He found that individual genera showed particular differences in their reproductive organs. Faasch (1935) describes in detail the alimentary canal and blood digestion in fleas.

Our knowledge of the internal anatomy of the adult flea is fragmentary and somewhat uncertain, and very few workers have gone even beyond describing the gross internal anatomy. Consequently, it is scarcely sufficiently detailed to throw any light on the affinities of fleas with other insects. A more detailed account of the internal anatomy of the adult is required.

### (c) Anatomy of the Early Stages

Of the early stages of fleas, the larva seems to have attracted the attention of many workers. Consequently, there exists a fairly extensive literature on its morphology, covering a period of many years, most of which deals with the external anatomy. It has been reviewed by Sharif (1937*b*), who gives a detailed and illustrated account of the internal anatomy of the rat-flea larva in the light of our existing knowledge of insect morphology. According to him the wing buds are first formed in the prepupa, and are of the simple type as in most Coleoptera.

Pupae have been briefly described by only a few workers (see Laboulbnèe 1872 ; Bishopp, 1931 ; Elbel, 1951), mostly dealing with the biology of fleas. Both their figures and descriptions are such that they can be applied to any species of fleas. Sharif (1940), who examined the pupae of seven genera of fleas, found that their sexes can easily be differentiated by the examination of terminal segments, and even the pupae of different genera can readily be distinguished by the configuration of these segments.

All fleas have free pupae which are completely unsclerotized, probably due to their being covered by well-spun cocoons.

Very little is known about the metamorphic changes that occur in the third larval instar and the pupal stage. Heymons (1899) gave a short account of the transformation of the mouth-parts of a flea, and his researches have greatly helped to elucidate the homologies of the mouth-parts of the adult. Wagner (1935, 1936*a*) described the changes undergone by the mid- and hind-gut of *Pulex irritans* Linnaeus during metamorphosis.

Several years ago the author worked on the metamorphic changes in the rat-flea, and a part of his investigations was incorporated in a previous publication (Sharif, 1937*b*), but a good deal of them has remained unpublished for lack of time. These investigations have impressed him that much valuable information about the affinities of fleas will be gained by this type of study, as many of the adult pulicine peculiarities are only developed within the pupa.

## III. ORIGIN AND AFFINITIES OF FLEAS

Ever since the taxonomic study of insects started, the origin and the affinities of the fleas have been debatable questions. Newman (1851), Haliday (1856), Kraeplin (1884), Wagner (1889), Packard (1894), Dahl (1898), Heymons (1899), Cholodkovsky (1914), Martini (1922), Martini and Burgarth (1923), Crampton (1931) and Tillayard (1935) have devoted their attention to these vexed problems. The theories put forward by earlier workers were not only

portion is slightly directed forwards. The mesonotum does not show any division into scutal and scutellar regions characteristic of the tergum of many wing bearing insects.

The metathorax of fleas is greatly developed owing to the part it plays in relation to the jumping mechanism. The tergum is strengthened by a number of internal apodemes, and pleura are "braced by well-developed ridges." The metepimeron is greatly developed; in some fleas it is the largest sclerite. It occupies the lateral and ventral regions of the first abdominal segment, which have no sclerotization of their own. It even overlaps the second abdominal segment. The first abdominal spiracle lies underneath the metepimeron, and according to Snodgrass (1946, p. 27), "It is difficult to explain the anatomical confusion encountered here, except on the assumption that the spiracle has retained its primitive abdominal position, and has been enveloped by the expanding thoracic epimeron...An apparent reason for the great size of the metathoracic epimeron is the presence of the large coxal muscle spread over much of the epimeral wall."

Even though the structure of thoracic segments has elaborately been described by Snodgrass (1946), Crampton (1931) and Fox (1941), still further elucidation of their structure is necessary. A detailed study of thoracic musculature, hitherto undescribed, will undoubtedly throw more light on homologies of the various thoracic sclerites and the affinities of fleas, as their thorax has undergone the least modifications.

(3) *The Abdomen.*—Wagner (1932, 1933) has demonstrated, by an involved argument, the presence of eleven abdominal segments in addition to the anal segment in adult fleas; but it has been shown by Ewing and Fox (1943), Sharif (1945) and Snodgrass (1946) that the abdomen is composed of only ten segments, and this number is easily discernible in the larval, pupal and adult stages of fleas. Embryological studies of Kessel (1939, p. 44) on fleas show the existence of eleven abdominal segments and the telson only in the early embryo; but the eleventh segment "is soon carried inward by the invagination of the proctodaeum, and becomes telescoped within the tenth segment". Possibly the so-called tenth abdominal segment in fleas is a composite structure including the eleventh segment.

The location of pygidium remains an open question. Most of the workers (Jordan and Rothschild, 1906, 1908; Rothschild, 1915; Martini, 1922) consider it as a part of the ninth tergum; but Wagner (1932, 1933) assigned it to the tenth, Sharif (1945) after refuting Wagner's arguments considers it as a portion of the ninth tergum. Snodgrass (1946) identifies it as a part of the tenth owing to the absence of any evidence of segmentation in the pygidio-proctiger region. Many workers have shown a line of demarcation

between the two, and Snodgrass has also observed it only in the male flea. He (p. 40) considers the pygidial plate "merely an enlargement of the precostal area of a simple tergum". The pygidium should not be homologized with the precosta of the following tenth segment, as the precosta can never be bigger than its tergum ; while the pygidium is definitely so. According to Snodgrass (p. 40), the dorsal pygidial muscles "are not present in female fleas", which may possibly account for the absence of division between the pygidium and proctiger in the female. Evidently, the pygidium is a part of the ninth tergum.

The structure of female genitalia owing to its simplicity has been worked out in detail by a number of workers (Lass, 1905 ; Martini and Burgarth, 1923 ; Snodgrass, 1946) ; but according to Snodgrass very little is known about the complex musculature of the bursa copulatrix and its duct, and the expulsory mechanism of the spermatic apparatus. The homology of anal stylets is unknown ; certainly, they are not cerci as is explained by Ewing and Fox (1943).

The male genitalia is an extremely complicated structure, and according to Snodgrass (1946, p. 3), "The complexity of the male intromittent apparatus is almost beyond belief". Sharif (1945) published a detailed account of the male genitalia of *Ctenocephalides felis* subsp. *orientis* (Jordan), about which Snodgrass says (p. 60) 'In an elaborate study of the male genital organ of the oriental cat flea, received too late for a full discussion, Sharif (1945) makes some very different interpretations from those given above. The external part of the organ is regarded as an extension from the ninth and tenth abdominal sterna ; the internal sack is therefore interpreted as a "phallothecal chamber", and the inner tube as the true aedeagus. A sperm "pumping apparatus" is described in detail, but no such structure has been observed, or, at least, so interpreted, by the writer'. Snodgrass has homologized the claspers with parameres as is the case in Mecoptera, Trichoptera and Nematocera ; but in fleas the claspers have become united with the ninth abdominal tergum. This assumption he bases on the description of formation of parameres in the prepupa of the rat-flea by Sharif (1937*b*) ; but in a later publication, Sharif (1945) suggests that copulatory rods are probably the parameres. At this stage it is not possible to agree with Snodgrass in considering claspers as parameres in view of our limited knowledge of formation of these structures. Further researches are required to elucidate this point.

According to Snodgrass (1946), the complex male apparatus consists of the aedeagus bearing a large basal apodeme and endophallus. He has failed to identify the periphallic structures with the ninth and tenth sterna, between which the genital complex lies ; this has led to his different interpretation from that of Sharif (1945). The structure identified by Snodgrass as aedeagus is

does not differ from the head of any other insect". This is also applicable to many other structures of fleas, provided we can understand them correctly. Mouth-parts of fleas have attracted the attention of many workers (see Landois, 1866; Packard, 1894, Heymons, 1899; Advisory Committee 1906*b*; Snodgrass, 1944, 1946); but so far their homologies have been moot questions.

Of the three stylets of the mouth-parts, the unpaired one has been designated hypopharynx by Packard (1894), Ewing (1929) and Snodgrass(1944), labrum by Heymons (1899) and Ewing and Fox (1943), labrum-epipharynx by Patton and Evans (1929) and epipharynx by Dampf (1945). Subsequently, Snodgrass (1946, p. 11) on a reconsideration has named it correctly the epipharynx, and according to him "A similarly developed epipharyngeal structure is not known to exist in any other insect". The ontogenetic studies on the mouth-parts of *Nosopsyllus fasciatus* (Bosc) by Sharif (1937*b*), reveal that the structure in question is the true epipharynx; this fact was, however, not realised by him when describing this structure. In the larva of this flea the epipharynx is absent, and the labrum is well developed; but in the third instar larva a bud is formed at the junction of the lower surface of the labrum with the upper surface of the buccal cavity, which outgrows the bud of the labrum. In the prepupa and the pupa both the labrum and the epipharynx are present; but the latter has far outgrown the former, and the medial unpaired stylet of the adult is formed within it.

The paired stylets have been regarded by Börner (1904) and by Snodgrass (1944, 1946), as lacinae of the maxillae. According to Snodgrass (1946, p. 13), the "articulation of the basal arms of the stylets on the lobes, and the origin of the protractor muscles of the stylets...within the lobes can leave little doubt that the stylets are the maxillary *lacinæ*". The study of the transverse sections through the head by Sharif (1952) reveals that the basal arms of mandibles, often called levers, do not articulate with the basal angles of the maxillary lobes, as suggested by Snodgrass; but only the distal ends of the levers are connected with the maxillary lobes by the soft peristomal membrane which also connects them with the labium. Only a part of the side of each lever lies embedded in the peristomal membrane, and its greater portion lies within the cranial capsule. The point of articulation between the basal arm of the mandible and the maxilla, as is mentioned by Snodgrass (1944, 1946), is not possible; for the base of the lever lies inside the cranial capsule and the part of the maxilla which according to him articulates with the lever lies outside it. The muscle designated by Snodgrass as the protractor of the lacinia is in reality the depressor of the galea. It is not possible to agree with Snodgrass (1944, p. 86) in that the basal arms of the paired stylets of the flea "have neither of the two usual mandibular articulations with the head, and, because of their position

between the maxillae, have no connection whatever with the cranial margin". Each mandible has the two usual articulations with the head, one through the lever arm on the membranized peristomal fossa and the other through the inner trabecula of the mandible below the free end of the hypopharynx.

The morphological significance of mouth-parts of the adult flea based on their ontogenetic development, partly described elsewhere (Sharif, 1937*b*) and partly to be published shortly (Sharif, 1952), should leave no doubt as to the mandibular nature of the paired stylets, as was suggested by most of the earlier workers (see Heymons, 1899; Kraeplin, 1897; Jordan and Rothschild, 1906). The large imaginal buds formed within the larval mandibles (see Sharif, 1937*b*, Fig. 79) develop into mandibular lobes of the prepupa, having quite an independent origin from those of the maxillae. Even the nerves supplying these two kinds of lobes are different. Three distinct centres of proliferation of ectodermal cells for the mandible, the maxilla and the labial palp close to each side of the mouth should provide a convincing proof of the independent origin of the mandible from that of the maxilla. Even at the time of adult formation within the pupal skin the mandible has a distinct origin, as indicated by distinct proliferation of its cells, from that of the maxilla. The forward movement of the latter has commenced even in the pupa. The forward location of the maxillae, a characteristic feature of fleas, their superimposition on the mandibles, different interpretations of the musculature of the mandibles and the maxillae, and wrong interpretation of mandibles as parts of maxillae by a few earlier workers have led Snodgrass to call them as lacinae. The presence or absence of mandibles in the adult fleas is a very important point for ascertaining their affinities with other insects.

(2) *The Thorax.*—Fleas have lost their wings; but they have utilized their legs as an efficient substitute. The thorax of fleas is in many ways different from that of the flying insects, from which they have certainly descended. The sternal and pleural sclerites of each of the thoracic segments have become fused; though the apodomes on the inner side indicate the lines of demarcation of the various component sclerites in many fleas.

The prothorax is composed of a tergum and a composite pleurosternal plate. Owing to the complete fusion of sternum, episternum and epimerum, it is not possible to define the limits of these sclerites in fleas, although Snodgrass (1946) and Fox (1941) have suggested their approximate lines of demarcation. The lateral compression of the head and the thorax has resulted in an unique extreme forward extension of the junction of the pleurosternite and the first pair of coxae; the sternum is far ahead of the tergum.

The mesothorax has not got the pronounced angulation between the tergum and the pleurosternal region found in the prothorax; but still its sternal

# FLEAS AND THE PART THEY PLAY IN PLAGUE

SECTION OF
BIOLOGY: ZOOLOGY, ENTOMOLOGY AND BOTANY

PRESIDENT :

Dr. M. SHARIF, D.Sc. (Panjab), Ph.D. (Cantab.), F.N.I., P.E.S. (I)
PROFESSOR OF ZOOLOGY, GOVERNMENT COLLEGE, LAHORE

PRESIDENTIAL ADDRESS

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## I. INTRODUCTION

MY first duty is to offer you my sincerest thanks for the honour you have conferred upon me by electing me to preside over the deliberations of the section of biology this year. It has been customary for the president to address the section on a subject to which he has devoted some thought and study. I have been interested in fleas for the past quarter of a century, and have, therefore, selected this subject for my address. Fleas are known to play an important part in the health, efficiency and comfort of a fairly large number of people throughout the world. The importance of fleas varies from being a pure nuisance to provoking flea allergy, plague, endemic typhus, tularemia, besides playing an important rôle as pests of live-stock, dwellings and warehouses.

In these pages I have endeavoured to give an idea of the work that has been done on fleas and have indicated the lines of further research. My intention is not to assume the rôle of a reviewer who must necessarily go through all the details of the subject in the stereotyped manner, but to make an attempt to interpret the many available publications, often conflicting, in the light of my own observations and to try to evolve some order out of the seeming chaos. Owing to lack of time and space it has not been possible for me to deal

with some important aspects of this vast and complex subject, which embodies within its domain a huge store of information in the published form. My vast and varied experience in the line in a way added to my difficulties in condensing the remarks within the compass of a short address like this.

## II. MORPHOLOGY OF FLEAS

Fleas are remarkable insects, as their morphology, in spite of the efforts of many workers, has not been adequately understood. The lateral compression of adult fleas necessary for their easy gliding through the hairs of mammals and feathers of birds has caused many morphological complications. This fact, often ignored, should be given due consideration in homologizing the various parts of these insects. Further complications arise from their acquiring parasitic mode of life in the remote past, when mammals, their fundamental hosts, first appeared in the Triassic period. The dependence of fleas upon their hosts is most marked, as they are the only holometabolous insects that need blood in their feeding stages, the adult and the larva.

### (a) External Anatomy of the Adult

We owe our knowledge of the external anatomy of the adult fleas to Karsten (1864), Landois (1866), Berté (1878), Wagner (1889, 1926), Rothschild (1898), Tiraboschi (1904), Jordan and Rothschild (1906, 1908), Advisory Committee (1907*b*), Patton and Cragg (1913), and many others who only give notes on the anatomy as applied to systematics.

A remarkable contribution to the anatomy of fleas has recently been made by Snodgrass (1946, p. 3), who has attempted "to interpret the skeletal anatomy of fleas, according to the general principles of insect morphology"; but in certain respects fleas have even defied him: he was forced to say about their morphology that "there are numerous peculiarities that strain the imagination for a plausible explanation". Owing to the extreme degree of specialization of fleas, no part of their external anatomy could possibly be mistaken for that of any other insect.

Our knowledge of flea morphology is far below the standard achieved in many other insects, even though after passing through series of errors committed one after the other, it has now taken somewhat correct shape. A detailed anatomy of different adult fleas is still greatly needed to homologize their various parts.

(*1*) *The Head.*—According to Snodgrass (1946, p. 3). "The head of the flea is a highly specialized cranial capsule, and most of its special features are peculiar to the Siphonaptera; but in its fundamental structure the flea head

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# FLEAS AND THE PART THEY PLAY IN PLAGUE

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BY

Dr. M. SHARIF, D.Sc. (Punjab), Ph.D. (Cantab.), F.N.I., P.E.S. (I)

PRESIDENT, SECTION OF
BIOLOGY : ZOOLOGY, ENTOMOLOGY AND BOTANY


PAKISTAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE
UNIVERSITY INSTITUTE OF CHEMISTRY
LAHORE

Table 1. *Showing the effects of different foods, when mixed with acid-washed sand, on the growth of the recently hatched larvae of the three Indian species of* Xenopsylla *at a temperature of* 25 ± 1° C. *and a relative humidity of* 80 %

| Species | Larval food used | Experiments tried | No. of larvae used | Larvae died in different active instars: No. | Sig. $\chi^2$ test | Larvae spun cocoons or formed naked pupae: No. of cocoons | No. of naked pupae | Total | Sig. $\chi^2$ test | Larvae reached the adult stage: No. | Sig. $\chi^2$ test |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cheopis* | B. | 3 | 150 | 145 | | 5 | 0 | 5 | | 5 | |
| *Brasiliensis* | B. | 3 | 160 | 160 | − | 0 | 5 | 5 | − | 0 | − |
| *Astia* | B. | 4 | 178 | 178 | + | 0 | 0 | 0 | + | 0 | + |
| *Cheopis* | W. | 4 | 200 | 125 | × × × | 75 | 0 | 75 | × × × | 54 | × × × |
| *Brasiliensis* | W. | 4 | 196 | 91 | × × × × | 105 | 0 | 105 | × × × × | 84 | × × × × |
| *Astia* | W. | 4 | 200 | 148 | × × × + × | 52 | 0 | 52 | × × × + × | 41 | × × × − × |
| *Cheopis* | B. and W. | 3 | 160 | 0 | × × × × × × | 1 | 86 | 87 | × × × × − × | 34 | × × × − × − |
| *Brasiliensis* | B. and W. | 3 | 155 | 0 | × × × × × × − | 0 | 75 | 75 | × × × − − × − | 15 | + × × × × × × |
| *Astia* | B. and W. | 4 | 182 | 76 | × × × × − × × × | 3 | 71 | 74 | × × × − + × + − | 44 | × × × − × − − × |
| *Cheopis* | B. and Y. | 3 | 170 | 0 | × × × × × × − − × | 131 | 37 | 168 | × × × × × × × × × | 164 | × × × × × × × × × |
| *Brasiliensis* | B. and Y. | 4 | 204 | 2 | × × × × × × × − − × − | 187 | 15 | 202 | × × × × × × × × × − | 197 | × × × × × × × × × − |
| *Astia* | B. and Y. | 2 | 85 | 0 | × × × × × × × − − × − − | 81 | 4 | 85 | × × × × × × × × × − − | 85 | × × × × × × × × × − − |

Table 2. *Showing the effects of different foods, when mixed with acid-washed sand, on the growth of the recently hatched larvae of the three Indian species of* Xenopsylla *at a temperature of* 25 ± 1° C. *and a relative humidity of* 80 %

| Species | Larval food used | No. of larvae and period in which they completed their active larval life: Larvae | Days: Range | Days: Mean | Sig. $t$ test | No. of resting larvae and period in which they reached the adult stage: Resting larvae | Days: Range | Days: Mean | Sig. $t$ test | No. of females and duration of their combined larval and pupal life: ♀♀ | Days: Range | Days: Mean | Sig. $t$ test | No. of males and duration of their combined larval and pupal life: ♂♂ | Days: Range | Days: Mean | Sig. $t$ test |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cheopis* | B. | 5 | 23–33 | 29·00 | | 5 | 12–18 | 13·80 | | 2 | 44–45 | 44·50 | | 3 | 40–44 | 41·67 | |
| *Cheopis* | W. | 75 | 25–59 | 38·89 | × | 54 | 14–26 | 19·61 | × | 38 | 41–75 | 54·18 | − | 16 | 45–65 | 58·06 | × |
| *Brasiliensis* | W. | 105 | 21–49 | 32·46 | − × | 84 | 13–24 | 17·13 | × × | 49 | 34–62 | 46·00 | − × | 35 | 39–65 | 49·57 | + × |
| *Astia* | W. | 52 | 44–80 | 64·62 | × × × | 41 | 11–32 | 16·73 | − × − | 30 | 60–112 | 80·17 | × × × | 11 | 68–85 | 76·45 | × × × |
| *Cheopis* | B. and W. | 160 | 13–21 | 15·22 | × × × × | 34 | 13–17 | 15·00 | − × × + | 27 | 26–33 | 28·89 | × × × × | 7 | 26–33 | 32·00 | × × × × |
| *Brasiliensis* | B. and W. | 155 | 13–31 | 17·74 | × × × × × | 15 | 15–19 | 17·60 | × + − − × | 9 | 31–38 | 33·00 | × × × × × | 6 | 28–40 | 32·50 | + × × × − |
| *Astia* | B. and W. | 106 | 20–40 | 30·63 | − × + × × × | 44 | 10–17 | 13·91 | − × × × + × | 29 | 33–48 | 40·48 | − × × × × × | 15 | 37–54 | 42·40 | − × × × × × × |
| *Cheopis* | B. and Y. | 170 | 8–13 | 10·92 | × × × × × × × × | 164 | 11–17 | 13·28 | − × × × × × − | 83 | 19–23 | 21·28 | × × × × × × × × | 81 | 25–29 | 27·11 | × × × × × × × × |
| *Brasiliensis* | B. and Y. | 202 | 10–14 | 11·95 | × × × × × × × × × | 197 | 11–18 | 14·35 | − × × × − × − × | 107 | 21–26 | 23·08 | × × × × × × × × × | 90 | 28–32 | 29·87 | × × × × × × × × × |
| *Astia* | B. and Y. | 85 | 10–14 | 12·24 | × × × × × × × × × − | 85 | 11–17 | 13·40 | − × × × × × − − × | 51 | 21–26 | 23·08 | × × × × × × × × − | 34 | 28–31 | 29·47 | × × × × × × × × × − |

Table 3. *Showing the measurements of adults of the three Indian species of* Xenopsylla *reared from larvae fed on different foods, when mixed with acid-washed sand, at a temperature of* 25 ± 1° C. *and a relative humidity of* 80 %

| Species | Larval food used | No. of ♀♀ | Length of females in mm.: Range | Length of females in mm.: Mean | Sig. $t$ test | Breadth of females in mm.: Range | Breadth of females in mm.: Mean | Sig. $t$ test | No. of ♂♂ | Length of males in mm.: Range | Length of males in mm.: Mean | Sig. $t$ test | Breadth of males in mm.: Range | Breadth of males in mm.: Mean | Sig. $t$ test |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cheopis* | B. | 2 | 1·31–1·67 | 1·490 | | 0·58–0·62 | 0·600 | | 3 | 1·35–1·67 | 1·490 | | 0·58–0·62 | 0·593 | |
| *Cheopis* | W. | 30 | 1·04–1·84 | 1·386 | − | 0·56–0·84 | 0·699 | − | 12 | 1·04–1·55 | 1·348 | − | 0·56–0·89 | 0·628 | − |
| *Cheopis* | B. and W. | 27 | 1·27–1·91 | 1·575 | − × | 0·67–0·89 | 0·788 | × × | 7 | 1·44–1·84 | 1·630 | − × | 0·58–0·87 | 0·717 | + + |
| *Cheopis* | B. and Y. | 61 | 1·76–2·24 | 1·952 | × × × | 0·84–1·04 | 0·950 | × × × | 61 | 1·80–2·12 | 1·964 | × × × | 0·72–1·04 | 0·877 | × × × |
| *Brasiliensis* | W. | 31 | 1·09–1·49 | 1·320 | + + × × | 0·58–0·71 | 0·643 | − × × × | 30 | 1·05–1·73 | 1·325 | + − × × | 0·53–0·75 | 0·587 | − + × × |
| *Brasiliensis* | B. and W. | 9 | 1·25–1·42 | 1·346 | − − × × − | 0·53–0·67 | 0·614 | − × × × + | 6 | 1·09–1·42 | 1·295 | − − × × − | 0·58–0·69 | 0·637 | − − − × + |
| *Brasiliensis* | B. and Y. | 87 | 1·48–1·88 | 1·688 | × × × × × × | 0·72–1·00 | 0·858 | × × × × × × | 67 | 1·52–1·88 | 1·678 | × × − × × × | 0·76–0·96 | 0·814 | × × × × × × |
| *Astia* | W. | 30 | 1·24–1·49 | 1·355 | + − × × − − × | 0·58–0·75 | 0·664 | + + × × + × × | 11 | 1·24–1·55 | 1·400 | − − × × − − × | 0·53–0·76 | 0·615 | − − + × − − × |
| *Astia* | B. and W. | 17 | 1·27–1·91 | 1·554 | − × − × × × × × | 0·67–0·89 | 0·794 | × × − × × × × × | 15 | 1·20–1·91 | 1·549 | − × − × × × × + | 0·62–0·87 | 0·720 | × × − × × + × × |
| *Astia* | B. and Y. | 51 | 1·76–2·16 | 1·962 | × × × − × × × × | 0·92–1·16 | 0·993 | × × × × × × × × | 34 | 1·84–2·12 | 1·968 | × × × − × × × × | 0·76–0·92 | 0·859 | × × × − × × × × |

**Key to abbreviations:** B., blood; B. and W., blood and wheat flour; B. and Y., blood and yeast; W., wheat flour; Sig. $t$ test, $t$ test of significance; Sig. $\chi^2$ test, $\chi^2$ test of significance; −, not significant; +, significant at 5 % level; ×, significant at 1 % level.

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